The Nutritional Requirements of Wild Scottish Red Deer (*Cervus elaphus* L.) Hinds for Winter Maintenance and Pregnancy.

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Ph.D.
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1978.

ABSTRACT.

I collected 19 pregnant, wild red deer hinds (females) over 14 February to 25 May, 1973, to investigate the extreme weight losses which then occur, since these seem to exemplify the poor productivity of Highland deer populations. Twenty-nine foetuses also were collected, from 18 January to 25 May, the last 19 being those of the collected hinds. Both hinds and foetuses were analysed by physical dissection and chemical composition determinations, and the results are presented and discussed.

The hind sample significantly decreased in body weight over the collection period, accompanied by a decrease in empty-body (ingesta- and conceptus-free) gross energy content from 130 Mcal (544 MJ) to less than 70 Mcal (293 MJ), a drop of around 50%. Empty-body fat content decreased from 11 to less than 3%. A 1 kg decrease in empty-body weight was accompanied by a drop of 3.74 Mcal (15.65 MJ) in body energy. Hind carcass data are compared with data from cattle, sheep and white-tailed deer, and hind body fat depots are discussed.

Foetal energy content rose at an average rate of 2.66 kcal/day (11.13 kJ) prior to mid-March (during the presumed middle third of gestation), and 64.1 kcal/day (268.2 kJ) afterwards. Foetal chemical composition is described, and found to be remarkably similar to that of white-tailed deer and, by deduction, to cattle and sheep, at equivalent gestational stages.

Having made assumptions of efficiencies of use, estimates are presented of the energetic cost of pregnancy,

and winter weight maintenance requirements.

An experiment was undertaken to measure the productive response of wild hinds to being winter-fed with a high-energy diet; because only one fed hind could be recovered for analysis the experiment was inconclusive.

This research and other recent published work lead me to the conclusion that Highland red deer are well adapted to living off body energy reserves in winter, and that level of summer dietary energy intake probably is the most important single factor presently inhibiting Highland red deer productivity.

ACKNOWLEDGEMENTS.

As is always the case with such projects, the work reported in this dissertation might never have reached a conclusion but for the help given to me, by many people.

I would like to thank sincerely Dr. W.E.S. Mutch and Dr. J.D. Lockie for their critical comment and continuous encouragement and support, without which this thesis may well have not been completed.

Thanks also to all the others who helped in their own ways, and in particular:
to Mr. Jim Fraser of the Carcass Evaluation Unit, and Dr. P. Crooks of the Central Analytical Laboratory, both of the East of Scotland College of Agriculture for their work during the dissection and chemical determinations;

to all the estate staff at Glen Feshie and Killilan who helped with the collection of the hinds and foetuses; to Dr. Brian Staines, of I.T.E., Banchory, for allowing me to tag along at Glen Feshie; to Mr. George Nairn, stalker at Corrour; to the proprietors of Braulen and Monar estates, for allowing me to work on their ground; to the proprietor of Erchless estate, for providing me with a place to live during the feeding experiment; to Mr. John Fraser and Mr. Sandy Duncan for allowing me to get in their way during the stalking; to Dr. R. Muetzelfeldt for providing me access to the computer programme with which the results were analysed, and for his help with the programme.

Thanks to Mr. John Simpson and Mr. Iain MacLaren for the long hours they put in trying to help, at very great expense to themselves.

Especial thanks to Mr. Baxter Cooper, Mr. A.W.A. Russell, and Mrs N.L. Jennings (née Dekker), for their very great help, in all kinds of ways, at all kinds of times.

I must also offer sincere thanks to Mrs. Brock for typing this thesis.

Finally I must thank the Highlands and Islands Development Board for providing most of the money for this research.

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INTRODUCTION

The red deer (Cervus elaphus L.) has been a part of the social and economic life of man in Scotland, and especially in the Highlands, since at least the late Stone age. The numbers of animals and the size of the area they grazed over at different times has been outlined by Lowe (1961). Estimates of the amount of land the species presently occupies vary (cf Darling & Boyd, 1964; Lowe, 1961; Red Deer Commission, 1973). It is generally accepted, however, that on at least 1.0 million hectares (2.5 million acres) of Scotland red deer are the only biologically-productive resource seriously exploited by man. Mather (1972) estimates that deer share a further 0.25 million ha. with other forms of land use; the total area used by red deer may represent 37% of the land area of Scotland.

The desirability of so much of the country's land being unexploited except for the culling of deer is the subject of much debate. Mather (1972) states that "... there is still a widespread belief in some quarters that they [red deer] represent underuse if not misuse of considerable areas of land." The arguments of those who consider deer shooting estates ("deer forests") to be misuse of land are often presented in vague, frequently sociological, political or highly emotional terms. Notwithstanding these arguments, scientists must attempt to establish which system, or integration of systems, of land use is biologically and economically the most productive, on a sustainable, long-term basis, while not leading to any irreparable ecological damage. The fact that extensive systems with domestic grazing animals have in the past been tried on much of the land that the animal now occupies, and have been shown to be commercially not viable,

supports the view that a production system based on the red deer deserves serious scientific investigation. Once gained, the result of such investigation at least will be available for consideration when future decisions are taken concerning Highland land use of public, or private, property.

Although the stalking of red deer has been the main pursuit, when not the exclusive pursuit, of such a large area of the Highlands since the middle of the last century, (cf Lowe, 1961; O'Dell & Walton, 1962; Darling & Boyd, 1964), the animal has been subjected to virtually no scientific research until quite recently. Cameron (1923) carried out some private investigations early in this century, but little further was undertaken on a large scale until Fraser Darling began the Red Deer Survey in 1952. In 1957 the Nature Conservancy began investigations into deer population dynamics, and since then the animal has been increasingly the object of scientific study. In 1970 a research project was begun by the Rowett Research Institute and the Hill Farming Research Organisation (HFRO) into the feasibility of producing marketable venison, by the domestication and management of red deer by traditional husbandry methods. This programme has since resulted in the publication of information about some aspects of the productivity of the species in the domestic environment (Blaxter et al., 1974), and the results of its various related research topics should produce valuable knowledge concerning the general biology of the red deer. The intensive husbandry system may in fact become established with commercial viability in parts of the Highlands with better-quality vegetation, moderate weather and easy access. But if attempted on that large portion of the region - which is at high altitude and has poor-quality vegetation combined with severe weather and limi-

ted accessibility, a deer husbandry system seems no more likely to achieve financial success than the sheep and cattle grazing systems tried in the past.

An alternative method of increasing the economic productivity of the Highlands is the improved management, in an extensive manner, of the red deer as a free-roaming, relatively wild creature. However, if such a system is to be guided by scientific knowledge, further research is required. I therefore considered it highly desirable that the factors inhibiting the productivity of wild red deer be examined, and that research be undertaken into ways of increasing that productivity.

The production rate of a deer herd is in part determined by its:

(i) reproduction rate;
(ii) "recruitment" rate;
(iii) individual growth rates; and
(iv) natural mortality rate.

In attempting to assess the productive potential of Highland deer, it is instructive to compare these rates, as observed for Highland herds, with those of red deer populations elsewhere.

Various rates concerned with reproduction can be described for an animal population. Conception or pregnancy rates describe the number of females in a given class (e.g. age, or lactational state) which conceive and become pregnant. Birth rates describe the numbers of young actually born. "Recruitment" rates are generally used to describe the number of young animals joining the adult (as defined by age or reproductive ability) population. Pregnancy and birth rates are often very nearly equivalent for intensively managed domestic animals, and

the difference between birth rate and recruitment rate is largely determined by management decisions (e.g. the number of young to sell or slaughter before they reach reproductive status, etc.). This is rarely, if ever, the case in wild animal populations. The limited data available suggest that the birth rate in a Highland deer herd may be lower than the conception rate, due to relatively high inter-uterine mortality, or foetal resorption by the mother. Recruitment of breeding females into the adult population is also often considerably lower than might have been expected from the birth rate. In order to assess the productive potential of a herd on a long-term basis, the recruitment rate of sexually mature hinds (females) into the adult population must be known. Unfortunately, accurate estimates of recruitment rates into Highland herds are very difficult to make. The Red Deer Commission (RDC) has published figures of calf/hind ratios arrived at during counts taken in a variety of areas of the Highlands. These calf/hind ratios are sometimes described as recruitment rates, but such usage can often be misleading. Most Highland hinds do not become sexually mature (capable of ovulating) until they are two years old, thus "dropping" their first calf around the time of their third birthdays (Darling, 1937; Lowe, 1961; Mitchell, 1969; Mitchell et al., 1971). Thus recruitment of sexually mature hinds can only confidently be estimated from calf/hind ratios when the sex ratio of calves and the mortality occurring between the times of a count and first calving are known or accurately estimated. Calf/hind ratios in the Highlands are expressed from counts often taken during the spring months, the very period when most of the natural mortality occurs (Lowe, 1961; Mitchell et al., 1971), and when calves orphaned during the culling season, and that

therefore have a reduced probability of surviving until summer, are still present. Since mortality is particularly high among young animals, use of a calf/hind ratio would result in a considerable overestimation of adult recruitment if a large number of calves were to die after they had been counted. Using calf/hind ratios to try accurately to estimate recruitment is also questionable since the counts are often made from long range visually. The possibility therefore arises of misclassifying hinds as calves, or vice versa (such misclassification is particularly possible the year after a severe winter, when the growth of many yearlings has been stunted, making them nearly the same size as the next year's calves).

In spite of the unreliability of estimating recruitment rates from calf/hind ratios, I have done so here simply for the purpose of rough comparison. Estimates of calf/hind ratios in the Highlands can be seen to vary from year to year and from one locality to another (cf Mitchell, 1969; and the RDC Annual Reports for the years 1972 to 1977). However, 35-37 calves per 100 hinds is probably acceptable as an estimate of an average for the region. In contrast, Caughley (1971) tells of a suggested ratio of 51 calves/100 hinds in an area of New Zealand. Ratios of over 60 calves/100 hinds seem to be common for deer living in deciduous woodland in Continental Europe (Mitchell, 1969; Phillips & Mutch, 1972). Semi-wild park deer at Warnham Park, Sussex, were reported to have a ratio of 66 calves/100 hinds in 1968 (Mitchell, 1969). Blaxter et al. (1974) report a birth rate of 92% for hinds at the Rowett Institute/HFRO experimental deer farm at Glen Saugh, Kincardineshire: it has not been reported whether all these calves survived until the following year. While the use of the above-cited ratios to compare recruitment rates between

those of Highland deer and populations elsewhere is not strictly legitimate, it does suggest that the recruitment rates of Highland herds tend to be lower than those of deer found in better habitats.

A lack of strictly comparable sets of measurements makes it difficult to compare growth rates and average mature body size between red deer populations. The weights recorded and published vary from live-weights to those of carcasses cleaned to a lesser or greater degree. The comparison of biomass production as exhibited by growth is further complicated by the fact that, to be strictly comparable, populations must be of similar age structure (Caughley, 1971). This is necessary because red deer may take up to five years to reach their maximum mature body size. An average weight determined from a sample of a population composed mostly of mature animals therefore might be greater than that from a population of mostly young animals simply because the majority of the latter group have not yet attained their maximum size. Nevertheless, I have calculated from data collected by the Nature Conservancy throughout the Highlands (Mitchell et al., 1971), that an average "larder" weight (carcass weight minus the weight of the offal and some blood) for stags (males) aged between two and ten years old would be around 80 kilograms (kg). Using Mitchell's (1969:25) conversion factor, I estimated the live-weight of such an "average" beast to be about 112 kg. The same method used to estimate live-weights of "representative" stags from Cambden Park, Galloway and Warnham Court, Sussex gives figures of 192 kg and 224 kg respectively (data taken from Whitehead, 1950). Application of the method to data presented by Phillips and Mutch (1972), gathered from eight areas of Western Europe, estimates average two to ten year old

stag live-weights of from 194 to 259 kg. Similar differences in average live-weights can be demonstrated between those of Highland hinds and those from populations elsewhere. In spite of the possibility of the differences in average mature body weights being in some part due to differences in the ages of the animals making up the samples, there is no doubt that the average maximum body sizes and weights of Highland stags and hinds are smaller and lower than those of deer from better habitats. Because of lack of data I have not tried to compare growth rates of Highland deer with those of animals from elsewhere. However, Blaxter et al. (1974) reported that calves at their experimental deer farm which had been given supplementary winter feeding had achieved live-weights which were around 20 kg heavier than those of wild calves of the same age. Since the calves used had all come from the Highlands, or had been born of mothers which did so, these findings show that the growth rates of wild Highland deer are lower than their genetic potential.

Some quantitative data on natural mortality rates of Highland deer populations have been collected by workers of the Nature Conservancy (Lowe, 1969). The figures show that mortality rates can vary considerably annually. The vast majority of natural deaths occur in the late winter or spring, and are consistently highest among the youngest and oldest age classes. Cooper (1971), in his study of mortality in western Sutherland, was unable to identify a particular single factor, responsible for the majority of natural deaths he observed to which he could assign a proximate cause, but rather described them as the result of what he called the "starvation/malnutrition/disease complex". Anderson (1972) found very high correlations between certain winter weather parameters and annual variation in the numbers of deer of various age and sex classes

found dead on the Isle of Rhum. It was not possible to determine the extent to which severe weather caused death directly by its effect on the animals themselves, as opposed to its indirect effects on the nutritional quality and availability of the vegetation on which the deer feed. The concentration of most mortality in late winter or spring, and amongst the youngest and oldest animals, has led Mitchell et al. (1971) to the opinion that inadequate winter nutrition is probably the main factor responsible for natural mortality of wild Highland deer. Whatever its cause, natural mortality reduces the biological, and hence the economic, productivity of the deer herds. The characteristics of the mortality mentioned above (its annual variability, and concentration in particular age classes at a particular time of year), and their similarity to those of deer populations in America which have been successfully combatted (Cheatum, 1951; Cowan, 1950; Klein & Olson, 1960; Severinghaus, 1951), suggest that management practices may be employed to reduce Highland deer mortality, thereby increasing the productivity of the system.

The deer counts and studies of population dynamics that have been and are being carried out by the Nature Conservancy, the Institute of Terrestrial Ecology, and the Red Deer Commission, are providing information on the productivity of wild Highland red deer as presently "managed". It is virtually a misnomer to refer to the present situation as a ssystem of management. The only management technique being practiced on most Highland deer forests is the annual shooting of a somewhat arbitrarily arrived-at percentage of the assumed population. On a few estates deer, usually stags, are furthermore being fed during some or all of the winter. The feeding tends to be on a level and of a type of feed determined

solely by proprietors' or stalkers' whims, or the price of foodstuffs, rather than at a rate and of a type best suited to meet the animals' requirements.

The present lack of virtually any kind of scientific management of Highland red deer must tempt one to agree with those "quarters" cited by Mather earlier, at least to the extent that red deer may represent the ".... underuse .... of considerable areas of land". At present red deer are probably somewhat, perhaps even grossly, under-exploited as a productive resource. One cannot necessarily blame the present proprietors of the land for the situation, however. Until only very recently there have been few scientifically established management proposals to employ. The recommendations of the Red Deer Commission have now contributed to the marked increase in the numbers of deer being shot in the last few years. The deer husbandry experiment at Glen Saugh may also lead to a future intensification of deer management in some areas of the Highlands. I believe, however, that large areas, particularly in the Grampians, Cairngorms and North and West Highlands, are of an ecological nature such that, combined with the economic expectations of modern society, no capital or labour intensive system will achieve financial success if attempted there. I therefore felt that research should be directed towards the development of techniques to be used in an extensive management system which could optimise deer production on these areas. At the time that I was considering the choice of a research topic (1972) members of the South Ross Deer Unit were engaged in investigating ways of improving the economic production of such areas, especially through more efficient assessment of population dynamics, and by more efficient harvesting (their recommendations have since been published in

Mutch et al., 1976). I therefore decided to direct my research towards possible methods of increasing the biomass production of essentially wild deer.

The low reproduction and recruitment rates, small mature body size, and periodically high natural mortality rates, suggested to me that the dynamics of their annual energy regimes might be largely responsible for the relatively poor biomass production of wild Highland deer. The assumed poor quality of the nutritional input from hill vegetation, combined with the high environmental output demands, appeared liable to leave little energy surplus from body maintenance for the productive processes. Improving the energy status of the animals, either by improving their energy intakes through improved nutrition, or by decreasing environmental energy loss by the provision of shelter, seemed likely therefore to improve production in some if not all its aspects. The biological productivity of Highland deer herds is unlikely to be inhibited by a lack of stags capable of breeding, however, even at the present moment. The herding together and serving of a number of hinds by one stag during the rut (mating season) is well known, and has been studied recently (Lincoln et al., 1970; Blaxter et al., 1974). Since the sex ratio in most Highland areas does not depart much from 1 stag: 1 hind, such behaviour results in a considerable number of non-breeding males. Mitchell (1973) found that sexual maturity is reached by most Scottish stags as yearlings or two-year-olds: over the period October to February, during which time the rut partially occurs (it sometimes begins as early as August), most two-year-olds and all stags aged three or older that were examined by him were fertile. A large proportion of the stags which do not breed every year therefore

must be able to do so. I therefore decided to investigate first the nutritional, and especially the energy status of wild hinds over the critical winter period. Lack of time, and technical constraints ruled out an investigation into the effects of shelter on deer energy expenditure; instead I proposed to use the knowledge gained about winter energy status as the basis of a feasibility experiment which would try to increase the biomass productivity of wild deer by feeding them on the open hill.

CHAPTER 1. The Inhibiting Effects of Inadequate Nutrition on Wild Highland Red Deer Productivity.

1.1 The importance of insufficient dietary energy as an inhibitory factor.

Losses in body weight during the winter months are characteristic of Highland red deer populations (Mitchell, 1971; Mitchell et al., 1972; 1976). From a sample of 90 'adult' (at least two years old) hinds which were collected over a twelve month period from the Isle of Rhum, Mitchell (1971) found that body weights in early spring were only 74 to 77% of the maximum weights recorded during October. Similar over-winter losses have been observed in North American white-tailed deer (Odocoileus virginianus borealis: Hoffman & Robinson, 1966; Silver et al., 1969), red deer in continental Europe (Eickhoff, 1957), and domestic cattle and sheep (see Allden, 1970). Such losses in body weight reflect a survival adaptation whereby animals accumulate body tissue when their nutrient supply is sufficient, and katabolise this tissue when food is scarce. It seemed likely that the weight losses undergone by Highland red deer must be due largely to the katabolism of body fat, necessitated by an insufficient intake of dietary energy. Low productivity in domestic livestock is often due to an insufficient intake of dietary energy rather than to diet deficiencies of proteins, minerals or other nutrients (Blaxter, 1956; in Allden, 1970). Blaxter (1962) has pointed out that inadequate supplies of nutrients other than energy rarely inhibit ruminant production unless energy is available in sufficient quantity to meet requirements. I therefore proposed to concentrate in my research on the energy status and needs of wild hinds, and in the discussion that follows, the term nutrition and its various adjectival forms, except when otherwise stated, are used synonymously with

dietary energy.

1.2 Effects on growth.

Many studies have shown that the level of nutrition can affect the growth rates of young deer of the genus Odocoileus (e.g. Cowan & Wood, 1955; Julander et al., 1961; Verme, 1962; 1963; Murphy & Coates, 1966; Thompson et al., 1973; Smith et al., 1975), and also of red deer (Dzieciolowski, 1969; Bruggemann et al., 1973; Blaxter et al., 1974). Wood et al. (1962) noted that the calves of many wild populations of the genus Odocoileus cease to grow during the winter months, presumably because of an inadequate intake of nutrition, and Highland red deer calves experience a similar over-winter growth check (Mitchell et al, 1971), presumably for the same reason. The experimental work of Blaxter et al. (1974) and the lactation study of Arman et al. (1974) suggest that the poor quality of hill vegetation in the winter inhibits the growth of Highland calves both because of its low nutritive value when eaten by the calf, and also because it results in low lactation levels by the dams. The effect of level of nutrition on milk production may depend on an animal's previous lactational history, however. Allden (1970) cites several studies of milk production by dairy cattle showing that although a low plane of nutrition during rearing may result in a reduced milk yield in the first lactation, subsequent yields become superior to those of cows reared on higher nutritional planes. Allden states that there is no evidence to suggest that the milk yield of sheep raised on a low plane of nutrition subsequently surpasses that of ewes raised on a higher plane, however. As neither Blaxter et al. (1974) nor Arman et al. (1974) report on subsequent yields by their hinds, it remains

to be seen how level of nutrition affects red deer lactational levels in the long term. From the evidence with white-tailed deer, it seems likely that the effect of poor nutrition on lactating red deer is an inhibition of the amount of milk produced.

Although the rigours of the Highland climate may have exerted considerable selection pressures on the red deer living there towards small stature, it is likely that many presently, because of the annual occurrence of an inadequacy of nutrition during the winter, do not achieve their individual potential size. That this is so is suggested by the very large body sizes attained by the descendents of Highland deer introduced into areas of New Zealand which have vegetation of higher nutritive quality, and also those of deer which have colonised recently-planted woodland in the Highlands. Whether or not Highland hinds would increase their stature if provided with improved winter nutrition was a question I proposed to try to answer. According to Allden, there was no evidence in 1970 that cattle would not do so, but it was possible that a low plane of early post-natal nutrition might lead to smaller adult body size in sheep.

1.3 Effects on reproduction.

Chapman (1974) has pointed out that deer productivity rates can be affected by: "... age structure of the herd, age at which puberty occurs, ovulation and conception rates and their variation with age, gestation period, fecundity, foetal survival and sex ratio of the offspring". Additional factors are the survival rates of hinds until date of first calving, and survival rates of subsequent hind age classes. Some of these factors affect annual productivity, while others affect long-term potential. Excepting herd age

structure, there is some evidence to suggest that all of them can themselves be affected by level of nutrition.

1.3.1 The onset of puberty.

The onset of puberty in cattle appears to be linked with attainment of a particular weight, and to be relatively independent of age (Allden, 1970), but whether this is so for sheep is not known. Oestrus in both sheep and red deer appears to occur only during a part of any given year, and individuals may possibly achieve the physiological condition necessary for the onset of oestrus but not ovulate because of the temporal season. If so, this may partially explain the wide variation in age of onset of first oestrus observed in both sheep and deer.

Many observations of and experiments into the affects of nutritional plane on attainment of puberty by deer of the genus Odocoileus have been made in North America. Julander et al. (1961) noted that on what they classified as "good" summer range in Utah, U.S.A., all mule deer (O. hemonius hemonius) yearlings were pregnant, while only 60% of the yearlings on "poor" range were. Julander and his colleagues proposed that comparative differences in the productivity of the youngest producing age classes (which would be a result partly of the number of females which had attained puberty) are more sensitive indicators of differences in quality of the vegetative resource than are comparisons of reproduction rates of older age classes.

Ransom (1967) found that the number of white-tailed deer yearlings which had attained puberty in two areas of Manitoba, Canada, were considerably lower than the numbers elsewhere, although the rates of ovulation by older animals were similar in all areas. The fact that some fawns (calves) from an

area where no yearlings were pregnant were larger than those in other areas which were, led Ransom to postulate that some particular nutrient must be required for the attainment of puberty.

Verme (1962, 1965, 1967, 1969) carried out numerous observations of and experiments into the role of nutrition in relation to reproduction by white-tailed deer in Michigan, U.S.A. In one six-year experiment on does (females) corralled outdoors, he found that all yearlings, fed an amount of commercially marketed deer pellets he considered to represent a "high plane" of nutrition, were pregnant, while nearly 50% of those on a "low plane" (receiving 30% less of the same pellets) were not. Since his animals were receiving simply different levels of the same feed, Verme's experiment throws no light on Ransom's proposal that intake of a specific nutrient or number of nutrients to a critical level is necessary for the attainment of puberty by white-tailed deer.

Darling (1937) observed that attainment of puberty (as defined by first conception, rather than oestrus) is often "delayed" in Scottish red deer hinds. Pregnant yearlings have been observed in Scotland (Staines, 1970; Guinness et al., 1971; Mitchell, 1973; Blaxter et al., 1974) and also in Norway (Wegge, 1975): Daniel (1963) reported that he had found hinds in New Zealand which had conceived when they must have been no more than five to seven months old. Mitchell (1973) has investigated variations in age of attainment of puberty between areas in Scotland, and found that while some hinds achieve puberty as yearlings, the majority do so as two-year-olds, and some do not do so until they are three or even older. Average age of first pregnancy is lower among herds grazing more nutritious swards, and this

suggests that improving the nutritive intake of hind calves would reduce the age at which onset of puberty occurs. It would appear that poor nutrition presently is depressing the potential productive rate of many Highland deer herds by delaying the age of onset of puberty, and hence first pregnancy, of some hinds.

1.3.2 Ovulation and conception rates.

Many studies of effects of nutritional plane on the reproductive performance of cattle and sheep are of limited relevance to the situation of wild ruminants, in that they have been made on animals which, after any experimental limitation of dietary intake, are kept on high planes of nutrition. It appears that both cattle and sheep may be slightly less productive over their whole life spans, if they have been reared on particularly high nutritional planes. However, the current effect of a severe limitation of nutrient intake on both species may be a failure to ovulate (i.e., to be barren).

Instances of barrenness are relatively common among populations of wild ruminants. Morton and Cheatum (1946) noted that the productivity of white-tailed deer in northern New York State, U.S.A., was lower than that of populations in the southern part of the state, and a higher occurrence of barrenness among northern does may have been part of the reason. Morton and Cheatum proposed that the difference was due either to the persistent effects of lower-plane winter nutrition, or "a prevailing deficiency of one or more dietary elements needed for a higher ovulation rate".

Severinghaus (1951) fenced in a herd of white-tailed deer in an area of New York where natural browse was abundant. After a high rate of increase for two years, the area had

become severely overbrowsed and a high over-winter die-off occurred "due to malnutrition". Productivity during the following two years was much lower than previously (0.43 young/adult female as compared to 1.9 fawns/doe before over-browsing), and Severinghaus could find no specific reason for the difference other than malnutrition resulting from the over-browsing.

Julander et al. (1961) in a study of mule deer in Utah, found that the ovulation rate of does from the "poor" range they looked at was only 67% of that for does from the area of "good" range, and again the difference appears to have been due to the poorer quality of the vegetative resource on the first area.

In Verme's (1969) experiment with white-tailed deer he found that some of his "prime-age" (2.5 to 6.5 years old) does on the low dietary plane were "unproductive" (i.e., they either did not ovulate, or failed to conceive).

It is a particular characteristic of Scottish red deer that up to 40% of sexually mature hinds are found to be not lactating and have no calf at foot during the period of the cull (mid-October to mid-February; Mitchell, 1973). These so-called 'yeld' (i.e., barren) hinds may have lost their calves and ceased to lactate between parturition (late May to mid-July) and the time when they are observed or shot, but Mitchell and Lincoln (1973) consider this to be unlikely as an explanation for the majority of hinds in this condition. Mitchell (1973) feels that the low pregnancy rates of 'milk' hinds (i.e., those which are lactating, and accompanied by a current year's calf) suggests that the majority of yeld hinds are so because they failed to ovulate or to conceive during the rut of the previous year. He concludes (1973: 284):

"... mature Scottish hinds often take a full year to recover from producing and rearing a calf. This long recovery from the effects of pregnancy and lactation suggests strongly that nutrition is the main (proximal) factor limiting the performance of red deer in the Scottish hill-land environment".

1.3.3 Gestation period.

Length of the gestation period is largely determined by the evolutionary process. Only minor variations occur between individuals or pregnancies, and are usually of little or no importance to domestic ruminants. However, even minor variations may be of some importance in wild populations where food resources vary considerably seasonally in quantity or quality. When newly-born animals have only a limited period during which their bodies are preparing for a season of environmental stress and low nutrient intake, even minor variations in birth date may be critical. Factors which can affect birth date (e.g. conception date and gestation length) may therefore come to assume some importance to such populations. Poor maternal nutrition appears to be such a factor in ruminants. Hutchison and Macfarlane (1958) found that among East African Zebu cattle (Bos taurus) kept under ranching conditions, gestations which ended in October on average were 3.0 days shorter than those terminating only one month later. Hutchison and Macfarlane assumed that the difference was due to the rapid decline in quality of the vegetation during the intervening 30 days, and hence a poorer level of nutrition being available to those beasts calving in November.

Experimental evidence that poor maternal nutrition can lead to longer gestation periods in ruminants was found by Verme (1965, 1969) in his experiments into the effects of nutrition on white-tailed deer productivity. He concluded

that poor nutrition of the mother resulted in gestation periods up to six days longer than were those of does on a higher plane of nutrition.

Average gestation length of red deer hinds which were kept corralled for study on Rhum was found to be 231 ± 4.5 days (Guinness et al., 1971), which is virtually the same as the figure of 233 ± 3.5 days reported by Prell (1938) for red deer on the Continent. The hinds studied by Guinness and her colleagues were provided with a diet superior to that available to wild hinds, and no investigation was made of possible effects of the level of maternal nutrition on gestation length. However, two hinds in the Rhum study became pregnant two years in succession, and in each case the gestation period of the second pregnancy was about seven days longer than the first one had been. One might hypothesise that this is evidence that hinds which have been pregnant the previous year, when exposed to the severity of Highland winter weather, require even better nutrition than was provided if they are to be able to maintain their body condition at levels needed for short pregnancies.

Mitchell and Lincoln (1973) have investigated conception dates of hinds in two different Scottish areas inhabited by red deer. They proposed from their findings that milk hinds tend to conceive later than do yeld hinds, but since they estimated conception dates from foetal weights, it is possible that their data instead were a demonstration of slower growth by milk hinds' foetuses. However, they also found a highly significant correlation between body condition (as assessed by the ratio of weight of the kidney to that of kidney plus associated fat) and estimated conception date, using data only from hinds shot during December. Data from the present

study show that, as is commonly the case with pregnant animals, foetal demands on the red deer mother do not reach an appreciable level until the last third of the gestation period. As early as December (when hinds would normally be three months pregnant at most), it is unlikely that the very low levels of energy and other nutrients supplied by the mother for foetal growth cannot be met by hinds even in very poor condition. Mitchell and Lincoln's finding that foetal weights from hinds in poor condition were less than those from better hinds in December therefore does indicate that the poorer hinds had conceived later. Mitchell and Lincoln are thus probably correct in their assertion that milk hinds, which are consistently in poorer body condition than are yeld hinds (in that they regularly have lighter body weights and lower body fat indices), tend to conceive later than do yeld hinds. Blaxter et al. (1974), in their studies in association with the feasibility of deer farming, also found that some of their hinds calved considerably later than did the majority and proposed that later conception was the explanation.

While it may be true that hinds in poor condition generally conceive later than do animals in better condition, the evidence of Verme (1965, 1969) on white-tailed deer, Hutchison and Macfarlane (1958) on cattle, and possibly that of Guinness et al. (1971) on red deer, indicate that free-ranging ruminants in poor condition due to poor nutrition may have longer gestation periods as well. Either occurrence, since it results in late birth dates, will tend to suppress potential long-term productivity, if it further results in later-born young having higher mortality rates during their first winter.

1.3.4 Fecundity.

Possible effects of maternal nutritional plane on the fecundity of sheep, among which multiple births are common, have been reviewed by Allden (1970). Twins and even triplets are also common among deer of the genus Odocoileus, and Verme (1969) assumed that improved nutrition increases the fecundity of white-tailed deer, although he did not present statistical data to support the assumption.

It appears that red deer generally are biologically and genetically adjusted to producing only one offspring per birth (in spite of the opinions of some members of the general public with an interest in deer, that twinning is more common than has been supposed). Chapman (1974) has drawn attention to the danger in assuming that twinning has occurred just because a hind has been observed in the wild with two calves, since it appears that fostering may occur in red deer. Mitchell (1973) relates five reported cases of twin embryos being found in hinds shot in Scotland: he states that from the reproductive studies of which he is aware this would give an apparent twinning rate of one in every 600 conceptions, but he feels that the real incidence in the wild must be very much lower. Guinness and Fletcher (1971) have reported the only recorded instance of the actual birth of twins to a red deer in Britain; the hind giving birth was one of those kept corralled on Rhum and provided with a better diet than that available to most wild deer. Further information on the possible effects of maternal nutritional plane in red deer may be forthcoming from intensively managed deer farms, but at present it seems unlikely that the fecundity of wild or extensively managed red deer will be much affected by nutritional plane.

1.3.5 Foetal survival.

Experimental evidence of effects of maternal nutritional plane on foetal survival in ruminants is limited, since people are understandably reluctant, on both humanitarian and financial grounds, to conduct experiments which might result in foetal death, particularly since to do so may well also threaten the life of the dam. Although a cynic might suggest that the above considerations apply with less force to wild ruminants, few rigorous scientific observations have been made of foetal survival rates in wild deer populations. A few cases of foetal atrophy have been recorded in white-tailed deer (Mansell & Cringan, 1968), but none has so far been reported in red deer. Several stalkers (professional deer cullers) have related to me how they have come upon the bodies of hinds which appear to have died during parturition, and if this were the case it might be considered as foetal mortality. Since these reports have been simply of finding carcasses with the foetus protruding, rather than of actually observing death of a hind while giving birth, it is possible that the foetus has been forced partially out of the uterus by decomposition gases, after the hind had died for some other reason. Blaxter et al. (1974) report the instance of human assistance being required in the delivery of a calf by one of the hinds studied by them, and had this assistance not been available, the calf and perhaps the hind would presumably have died. Blaxter and his associates also report that during their study three calves were stillborn, but do not offer a reason for the mortality. During calf catching operations carried out as part of the present study, I happened upon a newly-born calf which died minutes later due to a physical abnormality (the hole left by the umbilicus

was so large that the intestines protruded). A veterinary surgeon accompanying me said that with such a congenital defect death was unavoidable.

The frequency with which such fatal defects occur must be relatively low, since by comparing pregnancy rates with population reconstructions made from observed mortality data, Mitchell (1973) suggests that pre-natal mortality is rare among red deer from the areas which he has studied. Since the bodies of newly-born calves usually disapper (due to rapid decomposition combined with the activity of scavenging animals) within hours of death (Mitchell, pers. comm.), so that early post-natal mortality would be indistinguishable from pre-natal mortality, Mitchell's comparisons mentioned above also suggest that the incidence of such early post-natal mortality in the Highlands must be low.

During his study of two red deer populations in Norway, Wegge (1975) thought that little foetal mortality occurred. His opinion and that of Mitchell (1973) suggest that when red deer do become pregnant, the survival rates of their foetuses are high.

1.3.6 Sex ratio of offspring.

Whether or not the sex ratio of offspring of several animal species is affected by any factors other than chance has been the subject of occasionally fierce controversy. Various possible controlling factors have been proposed: for instance it has been suggested that there is a tendency in some species, including Homo sapiens, for the progeny of first pregnancies to be male. Lowe (1969) suggested that 'prime-aged' (six to ten year old) red deer hinds on Rhum tend to produce a greater proportion of female calves, and

Jensen (1967, in Chapman, 1974) thought that hinds in some areas of Denmark do so. Caughley (1971) has challenged the statistical validity of Lowe's data. Re-examining it using a different technique Caughley concluded that there was no significant statistical evidence of a departure from parity of the calf sex ratios of Rhum deer, and stated (1971: 378): ".... the significance of the results depends heavily on the selection of age classes designated as prime".

Verme (1969) analysed data on 190 'prime-age' (2.5 to 6.5 years old) does. He found that from does which produced 1.75 fawns per doe (which he therefore considered to have had ample pre-breeding nutrient intake, and to be in 'prime' condition), 43.2% of the progeny were male. For animals with a productivity of only 1.15 young per doe, "... because they were underfed during the rut..." (Verme, 1969: 883), 72.1% of the young were male. Verme concluded that statistical testing showed a highly significant difference "... between the proportion of the sexes born to mothers on low diet compared to those on high diet when bred." The lack of certainty that the animals Verme described as on a 'high' or 'low' dietary plane had indeed been subjected to these dietary regimes means that one must have reservations about accepting his results as conclusive. However, it makes good evolutionary sense for a population, when faced with poor or declining food resources, to have evolved a mechanism which would restrict the animals' rate of increase by reducing the number of potential breeders born. It remains to be shown that white-tailed, or red deer, respond in such a manner to poor maternal nutrition.

1.3.7 Survival of females until date of first reproducing.

The long-term productivity of any animal population is

dependent on the number of females which survive long enough to produce and successfully rear young. I hoped that my research might produce information which would be of use to persons trying to improve the productivity and hence harvest rates of Highland red deer herds on a sustainable basis. I therefore considered the recruitment rates of hinds into the breeding classes (i.e., those which are actually producing calves) to be of particular importance. It is generally acknowledged that such recruitment rates are 'low', but few reliable determinations of them have been made.

Several North American studies have established that mortality during the first year of life, before females have a chance to breed, can be very heavy in population of deer of the genus Odocoileus. Losses of 30% in Wisconsin (Dahlberg & Guettinger, 1956), 25% in Nova Scotia (Dodds, 1963), and 13% in Maine (Banasiak, 1964) have been reported for white-tailed deer, and losses of 39% for mule deer (O. hemionus hemionus) in Utah (Julander & Robinette, 1950). Studies of black-tailed deer (O. hemionus columbianus) have found first-summer mortality of young to vary from 4 to 31% between different areas (Taber & Dasmann, 1957), and from 23 to 69% between years in one area (Brown, 1961).

It has been pointed out above that Mitchell's (1973) data suggested that Scottish red deer seem to suffer little early post-partum mortality, and Mitchell et al. (1971) stated that they were unable to collect reliable data on the extent of first-summer calf mortality on Glen Feshie estate, in the central Highlands. Red deer calf mortality during their first winter can be high, however. Wegge (1975) estimated calf losses of two populations of Norwegian red deer to vary from 10 to 41%. Lowe (1969) reported an average annual calf loss of 37.1% from the Rhum population over the period

1957 to 1966. Mitchell (1969) cited a case where over 60% of the calves on a Highland estate died during a particularly severe winter. Beddington (1973), having developed a theoretical mathematical model to describe the population dynamics of the red deer on Rhum, arrived at the conclusion that such large die-offs must occur periodically if the low level of the population in later years is to be explained satisfactorily.

The variability and occasionally very high level of mortality of red deer calves in the Highlands mean that accurate estimates of recruitment into the breeding class cannot be made from pregnancy or birth rates alone. Follis and Spillet (1974) proposed that correlations of sampled pregnancy rates with subsequently observed calf/cow ratios of free-ranging elk (Cervus elaphus canadensis, a close relative of, if not the same species as, the red deer) may be developed to predict the productivity of herds eight months hence, but admitted that the reliability of a predictive method of this kind depends upon the assumption that pre- and post-puberty losses do not occur, or remain sufficiently constant so that they can be confidently estimated. Because of the high annual variability of both calf and post-puberty mortality shown by Scottish red deer herd, annual deer counts, calf/hind classifications and natural mortality assessments are required (in addition to knowledge of such factors as age of first breeding, average pregnancy rates and herd sex ratio), if one is to be able confidently to predict the effect of harvesting a particular number of stags and hinds, in any one season, on the subsequent numbers and productive capacity of his herd. (A further problem facing deer managers is that calf/hind ratios are susceptible

to errors of misclassification (i.e. of hinds as calves or vice versa). Lowe (1969) found that over a ten year period on Rhum, an average misclassification of 13% had occurred, although in only one year did the error exceed 10 per cent.

Although annual mortality of wild deer populations can be extensive, little is known about the relative importance of different possible causes, or indeed, even of the actual proximate cause, in many cases. This is largely due to the very high cost in man-hours required to be confident of having found the majority of natural deaths in a given population, and particularly in finding carcasses which are in fresh enough condition that a proximate cause can be assigned.

In a study of winter mortality of mule deer during a period of heavy snowfall in South Dakota, Harris (1945) found that 63% of the animals found dead were fawns. The majority of deaths had occurred in April, after the snow had melted and good vegetative growth was in progress. All the dead deer found had stomachs full of green grass and forbs, but still "showed definite signs of malnutrition".

Cheatum (1951) felt that malnutrition was the major cause of winter mortality of white-tailed deer in New York, but because some dead were found with "an adequate volume of food in their stomachs", he decided to check the carcasses for parasites and disease. He found that nearly all the dead deer were extremely emaciated, and had higher incidences of liver fluke (Fascioloides magna) and of lungworm (Leptostr gyles alpenae), than were normally found in deer shot during the hunting season. Many animals he examined also had congested lungs suggestive of pneumonia.

Severinghaus (1951), during his over-browsing by white-tailed deer experiment in New York, found that mortality of

fawns during the period between birth and their first winter seemed to be negligible, but was heavy during the winter.

Julander and Robinette (1950) stated that fawns had the highest mortality rate (11.9%) among the mule deer they studied in Utah. In contrast to the present evidence on red deer and the observation of Severinghaus on white-tailed deer first-year mortality, they found that most of the young mule deer mortality occurred before the fawns were a month old (they did not give a cause). In a further study, Julander et al. (1961) re-iterated that the majority of fawn deaths of mule deer in Utah occur soon after birth, and stated that the majority were due to 'malnutrition' (whether of the fawns, dams or both, they did not indicate).

Klein and Olson (1960) studied natural mortality of black-tailed deer (O. hemionus columbianus) populations on some islands off south-eastern Alaska, U.S.A. (islands are particularly good areas for mortality studies, since the search for bodies is obviously restricted to the land area, and the territory of the herd is more or less clearly defined). They proposed that 'starvation' was the major cause of mortality in the region. Mortality rates were highest among the fawns and the 'old' age classes: Klein and Olson postulated that much of a young animal's first-summer growth was of muscle and bone tissue, with reduced fat accumulation.

In a so far unique study, Cook et al. (1971) investigated the cause of death of young southern Texas white-tailed deer fawns, and were able to find carcasses within 1 to 48 hours after death had occurred, by means of radio transmitters, which had been attached to the fawns soon after birth. Book and his colleagues considered predators to have been involved in 82% of the 58 cases of mortality observed, and attributed

only 9% to starvation directly. They admitted, however, that even with their technique they were unable to assess the extent to which nutritional stress may have predisposed fawns to death from predation or disease.

Several of Verme's experiments with white-tailed deer (1962, 1963, 1967) have shown that heavy post-natal mortality of fawns can result from the dams having been on a poor level of nutrition during pregnancy. Death resulted from: fawns being born in a moribund condition; being born too small to suckle from a standing doe; not being allowed to suckle by their emaciated mothers; or from the mothers' milk production being delayed or even non-existent. Similar early post-natal losses due to poor maternal nutrition have been observed in elk (Cowan, 1950).

Cooper (1971), in an investigation of red deer natural mortality in north-west Scotland, was unable to identify any single proximate cause of death from what he called the 'starvation/malnutrition/disease complex'.

Lowe (1969) suggested that predation by golden eagles (Aquila chrysaetos) may have been the cause of 'about 13.4%' of red deer calf deaths on Rhum, but he was not always able to discern whether or not signs of eagles on the carcasses he observed had been made after death.

Anderson (1972) found by regression analysis that variation in winter weather factors explained 92% of the annual variation in the number of calf deaths over the same period studied by Lowe (i.e. 1957-1968). Anderson was unable to say whether the high correlation was due to effects on the quality of the herbage, direct effects on the animals themselves, or a combination of both factors. Wegge (1975) thought that the heavy mortality of red deer calves he ob-

served in Norway was due to 'inadequate nutrition'.

The subject of 'natural' (i.e. not intentionally humanly induced) mortality should be recognised as of particular importance to managers of Scottish red deer, in that not only does the natural death of an animal reduce the potential productivity of the herd (if the beast be female), but also because it usually is financially wasteful, in that no monetary return is recovered for the carcass. Natural deaths in Scotland are occasionally the result of accidents, such as a beast being struck by a car, or becoming entangled in a wire fence and starving, and relatively little can be done to avoid such incidents. Serious predation, other than by man, is absent (excepting perhaps by golden eagles, which one must tolerate for conservation reasons, and which in any case is relatively trivial compared to the major cause of Scottish natural mortality). Death caused by disease alone also seems to be relatively rare: McDiarmid pointed out that little research had been done by 1969 into the health of wild deer, but that they appeared to be remarkably healthy, compared to domestic ruminants. The search for diseases in red deer quoted by Blaxter et al. (1974) further confirms this appearance.

Lowe (1969) and Beddington (1973) have found a correlation between summer rainfall and the numbers of deer dying naturally on Rhum the following winter. The probable explanation for this is that high summer rainfall reduces the deposition of body fat, either by reducing available dietary energy, by necessitating increased energy expenditure during the summer, or a combination of both of these. Thus, after a summer of high rainfall animals would enter the winter with lower body reserves of energy with which to maintain themselves.

The vast majority of natural mortality in Scottish deer herds, and certainly the occasional occurrence of a very large number of deer dying, very much appears to be caused by the combined effects of poor nutritional intake, and severity of winter weather. Watson (1971) found a highly significant statistical correlation between the number of deer he found dead in an area of north-east Scotland, and the number of days when the ground was snow-covered. However, he found most of his carcasses in early spring (late March to mid-May). Harris (1945) also found that the heavy mortality among mule deer in South Dakota, during a winter of very heavy snowfall, in fact mostly occurred in April, after the snow had melted.

The rarity of snowfall on Rhum may have meant that its possible effect as a cause of mortality was not fully demonstrated, but the single weather factor most highly correlated with the death of Rhum deer of all classes, in the analyses done by me in 1972, was the winter mean lowest maximum temperature. Mean lowest maximum temperature was an arbitrarily-derived parameter (found by calculating the average of the lowest maximum temperatures occurring during the months November to May), chosen to allow rough comparisons to be made, between winters, of how low the temperature remained during the daytime (since maximum temperatures occurred during the hours of daylight). Similarly, winter mean lowest minimum temperature was derived as a rough indication of how cold it regularly got during the nights of a winter. The fact that mean lowest maximum was more highly correlated with numbers of deaths occurring than was mean lowest minimum, suggested to me that very cold temperatures might necessitate only slight increases in energy expenditure by red deer

(because their coats, possibly, are of such excellent insulative quality that they need only slightly increase expenditure to maintain body temperature); but that they need to experience relatively warm hours of daylight during which they can reduce the expenditure of body reserves, or even experience periods of positive energy balance. A winter in which the temperature during the daytime remained low would instead necessitate a more or less continuous expenditure of body reserves, so depleting them that insufficient would be left, by springtime, to enable the body to withstand any physiological stress which might occur (e.g. a sudden spell of bad weather, or the normal parasite load, or pursuit by a predator).

Regardless of the precise mechanism by which Scottish red deer succumb to the rigours of the winter weather, it seems likely that an improvement in their dietary energy intake must improve their ability to withstand it, and thus decrease the wastage due to natural mortality, and increase the productivity of the herds.

1.4 Nutritional requirements of Scottish hinds for winter body maintenance and for pregnancy.

In his major review of effects of nutritional deprivation on the subsequent productivity of sheep and cattle, Allden (1970; 1182) ended by saying: "Under the changing climatic environment of the field it is improbable that cattle and sheep could survive on diets which might influence adversely their future productivity. Thus feeding for survival would in itself ensure the stability of future productivity." It is probably true that the annual winter period of nutritional deprivation which wild Scottish red deer hinds suffer also does little physiologically to affect permanently their pro-

ductive potential. However, since undernutrition is presently experienced year after year by Scottish hinds, the 'current effects' of undernutrition, so easily dismissed by Allden, are achieving virtually the same effect; i.e. permanent inhibition of herd production. The importance of Allden's statement to red deer is that it suggests that, if provided with improved nutritional intake, wild hinds will respond by increasing their productive performance.

At present Scottish hinds survive on a diet of natural vegetation which, at least periodically, is so poor in nutritive quality that it often is insufficient to enable them to achieve the level of body condition necessary to ovulate, if they have reproduced successfully the previous year. In view of this, it perhaps seems surprising that they utilise this same diet so successfully to improve their condition when they are not lactating, as the marked superiority in condition of yeld over milk hinds shows that they do.[1] Possible explanations of this apparent paradox might be that:

(a) the efficiency with which red deer utilise dietary energy for pregnancy and/or lactation is poor, relative to

(b) the efficiency with which they utilise it for body maintenance and fattening. It may also be that

(c) the natural hill vegetation of some areas of Scotland is low or lacking (perhaps for only certain periods of the year) in some 'ingredient X' - a particular nutrient or nutrients which are required for ovulation, pregnancy or lactation.

1 Mitchell et al. (1976, 1977) have shown that at the peak of their condition, in late November, yeld hinds aged 5 to 10 years had an average larder weight (i.e. carcass less that of some blood, and of the alimentary tract) of 62 kg, compared to the average of only 49 kg for milk hinds of the same age range.

After a review of the experimental evidence then available (1965), the Agricultural Research Council (A.R.C.) proposed that the utilisation of metabolisable energy (ME) for maintenance by domestic ruminants is relatively constant at around 72 to 74%, regardless of the metabolisability of the diet. The efficiency with which ruminants synthesise fat varies widely, however, depending on the nature of the diet: Kellner (in A.R.C., 1965) showed that the efficiency of fattening was inversely related to the fibre content of a food; Blaxter (in A.R.C., 1965) later showed that the efficiency was just as well correlated with the metabolisability of a diet.

The efficiency with which domestic ruminants utilise energy during pregnancy is not known. The A.R.C. (1965) recommend that one assume weight gains due to pregnancy to be made with the same efficiency as for normal growth. However, the high increase in heat production by pregnant animals (the 'heat increment of gestation'), leading to maintenance requirements at the end of pregnancy of about 1.5 times those of non-pregnant cows (MacDonald et al., 1973) suggests that the overall efficiency of energy utilisation by pregnant ruminants may be considerably lower than is that of non-pregnant ones. Indeed, Rattray et al. (1974a) estimated the efficiency of utilisation of ME for pregnancy in sheep to be only 16.1 per cent.

The efficiency of energy utilisation for lactation is not well established for ruminants, since it is difficult to measure the energy used for lactation separately from that being used for other functions such as maintenance or growth. The A.R.C. (1965) proposed that a figure in the region of 70% was acceptable as a general value for both

cattle and sheep.

The fibre content of the red deer's natural food plants is probably higher, and the metabolisability lower than they are for the normal diets of many domestic ruminants, or at least of those which are intensively managed. However, fibre content and metabolisability of red deer's vegetative resource can vary with temporal season and age of the stand. The fibre content is probably lower, and the metabolisability higher when hinds are putting on fat (during the summer months: Thomas, 1956; MacDonald et al., 1973; Milne, 1974), than these factors are when hinds are pregnant (i.e. winter and spring). It may be therefore that red deer utilise the energy available to them for maintenance, fattening and lactation with similar efficiencies; but that the use of energy for pregnancy is lower, both because of the lower overall digestibility and nutritive value of their food resource during pregnancy, and possibly also because the process of gestation reduces the overall efficiency with which energy is used by pregnant animals.

The possibility that the absence or low incidence of some mysterious 'ingredient X', necessary for ovulation or for pregnancy, was responsible for the lower productivity of white-tailed deer in some areas, as compared to that in others, has been raised by Morton and Cheatum (1946) and more recently by Ransom (1967). Lack of such a nutrient is also a possible explanation or partial explanation of the variations in age of first oestrus and in pregnancy rates generally, which have been related between different areas within Scotland, and between Scottish deer productivity generally and that of populations elsewhere in the world. I therefore resolved to keep the possibility in mind when examining the data gathered

in my research. Scotland and the areas studied by Morton and Cheatum (northern New York State) and by Ransom (Manitoba) are marginal areas of the distribution of the deer species concerned (red deer and white-tailed deer), however. These regions also have winter periods of limited daylength, with relatively severe weather, during which vegetative growth virtually ceases, and the nutritive quality of the existing vegetation drops. It therefore seems equally likely that variations in deer productivity between areas in these regions might be due simply to critical variations between them in either the levels of dietary energy available during the summer, or during the winter; or in the environmental energy demand made by winter weather, or any combination of these factors. Therefore, rather than choose and then attempt to establish the effect of different dietary levels of any particular mineral, vitamin or trace element on deer reproduction, I felt justified in concentrating my research on the energy requirements of wild hinds for winter maintenance and for pregnancy.

The term 'maintenance requirement' can be used to describe the energy needed to sustain a variety of physiological states. The dramatic weight losses undergone by wild Scottishred deer hinds must bring them precariously close to death by the end of winter; yet usually most survive. These hinds must therefore have had available, from food, body reserves (and possibly to some extent from long-wave radiation), at least that minimum amount of energy required to perform the basic physiological functions necessary to maintain life. Such an absolute minimum amount of energy, which will vary with the size, age and physiological state of animals, and the environmental stresses to which they are subjected,

might be called the 'survival maintenance requirement'.

In their textbook on nutrition, MacDonald et al. (1973) state: "An animal is in a state of maintenance when its body composition remains constant, when it gives rise to no product such as milk and when it performs no work on its surroundings". Either the energy required to maintain the basic metabolic rate (BMR), as determined from such an animal, or that required to sustain an animal as determined by its fasting metabolic rate (FMR), is the amount often described in nutritional studies as the 'maintenance requirement'. As MacDonald and his co-authors point out, even domestic animals are so rarely in such a state that determinations of the nutrient requirements for it may appear to be of no practical value. They offer as justification of such determinations that they provide the basis for enabling one to employ a factorial method to estimate the total nutrient requirements of an animal.

Brockway and Maloiy (1968) and Maloiy et al. (1968) have reported on determinations of heat production by Scottish red deer hinds when in a state approximating that described by MacDonald and his colleagues as the maintenance state. The reports of their findings are rather unclear, but their results do demonstrate how heat production varies with body weight and ambient temperature. Unfortunately, since their animals had been kept housed indoors, and estimates of requirements based on spot determinations made at temperatures rarely occurring on the Scottish hills during the winter (viz., 8°, 18° and 28°C), their estimates do not go far towards establishing what the energy requirements are of wild red deer, on the open hill, over the winter.

More pertinent field studies of wild deer metabolism

have been carried out by Silver et al. (1969) and Ullrey et al. (1969, 1970) on white-tailed deer. Silver and her colleagues measured the FMR's of deer of both sexes which were penned outdoors over a twelve-month period in New Hampshire, and thus were exposed to normal winter temperatures and weather. The animals were presented ad libitum with natural deer browse for the area, voluntarily reduced their intake during the winter months, and underwent weight losses of 11 to 28%, similar to those experienced by wild red deer. An estimate of the energy required to maintain the FMR's Silver and her associates measured, therefore would be an approximation of the 'survival maintenance requirement'.

Ullrey et al. (1969) conducted an investigation of digestible energy requirements of pregnant white-tailed deer, and repeated their investigation (1970) in a subsequent year with a new group of 18 pregnant does which were penned individually outdoors in Michigan; they were thus subjected to the normal winter temperatures of from 1.1° to -9.5°C. The does were divided into three groups: one was fed ad libitum on a specially prepared pelleted diet, while the others were fed 75% and 50% respectively of the amount eaten by the first group. This resulted variously in body weight gain or loss, depending on the group. Having measured the gross energy and the apparent digestibility of the diet, and then regressing diet intake against body weight change, Ullrey and his colleagues were able to estimate the amount of apparently digested energy that would be required to keep their does at a constant body weight. This amount may be referred to as the body weight maintenance requirement or simply the 'body maintenance requirement', but should not be confused with the

body weight maintenance requirements determined from BMR or FMR measurements.

The determination of a body maintenance requirement by the method of Ullrey and his associates is particularly relevant to the needs of wild deer, since it is not the result of a spot determination made on a single animal, which has been kept indoors, at higher than winter temperatures, and fed on a weight maintenance diet; rather it is an average based on measurements made over a three-month period, on several different animals which were exposed to typical winter temperatures and weather conditions. I therefore considered undertaking a similar experiment to determine a body maintenance requirement for Scottish red deer hinds over the winter. I rejected such a course, however, because the facilities for such an approach were not available, and also because I did not then fully appreciate the value of it. Instead, considering the facilities which were available, I set out to analyse the physiological changes occurring in the bodies of pregnant hinds over the winter. I then proposed, from the changes observed by physical dissection and chemical analysis, to calculate:

(i) the body maintenance requirement ('body maintenance requirement' will be used henceforth in this report to mean the average amount of energy required daily over the whole of the winter to enable wild hinds, exposed to normal weather and engaging in normal activity, to maintain approximately constant body weight).

I further proposed, from the observation of the accumulation of energy and elements in the products of conception, to estimate:

(ii) the energy and other nutrients additionally required by wild hinds for the reproductive process.

CHAPTER 2. Collection and Physical Analytical Procedures.

2.1. The study rationale.

The first objectives of this research were to analyse the changes occurring in the physical and chemical composition of the bodies of wild hinds over winter and spring, and to observe the growth and deposition of energy and nutrients in the developing foetus. To achieve these aims the bodies of a minimum of two pregnant hinds were to be collected at roughly fortnightly intervals over the period January to May. Since Mitchell and Lincoln (1973) have estimated that the median conception data at one of the collection areas (Glen Feshie) is around the 19th October, and the period of giving birth (the calving season) is from late May until about the end of June, with a peak normally in early or mid-June, the hinds would thus be collected over a period coinciding with the last two-thirds of gestation. The open season for the shooting of red deer hinds in Scotland ends on the 15th February, so in order to carry out the collection plan it was necessary to obtain from the Secretary of State for Scotland a special licence to shoot red deer out of season (for the purpose of scientific research).

In the event, hinds were collected over a period of only 100 days, from the 14th February until the 25th May, 1973. This was so largely because the limited financial resources available for this project necessitated the curtailment of some part of it. Since the effects of winter undernutrition appear to be cumulative, I hoped that restriction of the period of collection of bodies of hinds would still provide a sample sufficient to demonstrate the nature and extent of these effects. Foetuses were collected, with data on the age, weights and physical condition of their dams, during January,

and from the bodies of the hinds collected from February to May.

Ideally, an investigation into the physiology of undernutrition would be of experimental design such that factors other than nutrition which could cause variation in the parameters studied would be eliminated. Animals would be studied that were of similar genotype, the same age and same original size and weight. Further, they would be exposed to the same environmental conditions and their intake of nutrients would be known. Unfortunately, such ideal conditions often cannot be achieved during studies of wild animals; the present study was in no way able to do so.

The reluctance of estate proprietors and/or their stalkers to allow their deer to be shot out of season forced me to collect animals from three different areas, and the hinds in the sample population therefore may vary genotypically. Furthermore, although the climatic conditions at two of these areas (Glen Feshie and Corrour) appear to be similar, those at the third area are obviously different (see section 2.2 below). It also appears that the environmental energy demand made on deer by similar weather conditions can vary, depending on the relative availability of both large and small geophysical features, and of vegetation, which the animals can use to find shelter (Mitchell et al. 1977). Physiological differences observed in my sample therefore may be due to different energy expenditures to meet environmental demands, rather than differences in the degree of undernutrition experienced. The vegetative food supply available also appears to be similar between two of the collection areas (Glen Feshie and Corrour) but that at the third (Killilan) is noticeably different (see section 2.2), and

the hinds collected therefore may have been subjected to different levels of undernutrition.

The only collection method which could be employed (ordinary deer stalking with a rifle) meant that it simply was not possible to select hinds which were of the same size, weight or age. The stalking of red deer (and particularly of hinds, which are often more wary than stags) on the usually completely tree-less, open Highland hills is beset with inherent difficulties. The wind (which if from behind the hunter will warn the beasts of his presence and cause them to flee), rain (which not only can be very uncomfortable, but also soon renders binoculars and rifle telescopic sights unusable), snow (which can make getting out on the hills difficult), bad light on overcast, short winter days (which can make spotting deer, and then being able to shoot them, difficult), lack of covered approaches and often very steep terrain to be walked over, must all be overcome often just to bring one within shooting range of red deer hinds. (It is an unwritten, but usually strictly complied-with, law in the Highlands that approximately 200m. is the maximum range from which a shot may be taken. The reason for this is largely humanitarian; to try to guarantee the clean killing of an animal with a single shot. My desire that beasts, when possible, be shot in the neck reduced this range to nearer 100m.) Because of the time required to overcome the difficulties mentioned, hinds had to be selected simply on the basis of appearing to be adult (4 to 10 years old), pregnant, and within shooting range. In any case, hinds normally cannot be visually classified into much finer age categories than 'young' (up to 3 years), 'adult' (4 to 10 years) or 'old' (greater than 10 years of age). The hinds

collected for this study ranged in age from 4 to 10 years (Table 2.1), and therefore might be expected to vary in size and weight, and conceivably in body conformation and composition, due to their variation in age.

Variations, in at least some of the physiological parameters that would be examined in the sample population, were expected to occur. Since it has been proposed in the introduction to this study that wild red deer are subject to undernutrition during the period studied, and that the effects of this undernutrition are cumulative over that time, I wished to be able to test statistically the significance of any physiological trends observed over the study period mid-February to June. I therefore proposed to investigate the relationship between observed variation and the passage of time by means of simple linear correlation and regression analysis. To do so necessitated the adoption of a numerical scale to represent the passage of time. The 14th February (the first day on which a hind had been collected) was an obvious starting date for such a scale. However, my first foetal samples had been collected during January, and I wished to be able to investigate changes occurring in both hinds and foetuses in relation to the same scale. The next obvious starting date, the first of January, was rejected, because hinds normally begin to lose weight before then (Mitchell, 1971; Mitchell et al., 1976, 1977). Instead, the first day a hind was collected (14th February) was designated "Day 1" for the hind analyses, and the date of first collection of foetuses (18th January) for the investigation of foetal growth.

The plan of collecting two hinds and their foetuses every 14 days was not adhered to strictly (see Table 2.1).

Table 2.1. Identification number, date collected, place of collection, weights, age, and parity (whether milk, ie, lactating, or yeld, ie, not lacating) of the 19 hinds collected and examined.

HIND	DATE COLLECTED	PLACE COLLECTED	LIVE WT.[1] (KG)	EMPTY-BODY[2] WT. (KG)	LARDER WT.[3] (KG)	AGE	PARITY
17	14.3.73	Corrour	73.2	53.8	48.5	7	yeld
18	7.3.73	Corrour	62.4	47.0	42.8	5	yeld
19	7.3.73	Corrour	74.4	53.9	49.5	7	yeld
20	26.3.73	Glenfeshie	59.6	42.9	39.0	5	milk
21	26.3.73	Glenfeshie	68.8	50.3	46.8	5	yeld
22	26.3.73	Glenfeshie	68.0	48.5	45.0	6	yeld
23	28.3.73	Glenfeshie	61.8	43.4	40.4	9	milk
24	28.3.73	Glenfeshie	72.0	50.4	46.8	8	milk
25	28.3.73	Glenfeshie	61.3	46.0	42.7	4	yeld
26	28.3.73	Glenfeshie	60.2	44.8	40.9	7	yeld
27	29.3.73	Glenfeshie	70.0	49.5	45.4	8	yeld
28	30.3.73	Glenfeshie	?	51.7	47.2	10	milk
29	30.3.73	Glenfeshie	74.4	53.4	48.6	8	yeld
30	3.5.73	Killilan	78.4	53.5	48.0	8	yeld
31	4.5.73	Killilan	65.7	45.6	40.9	6	yeld
32	9.5.73	Corrour	57.6	39.8	36.1	6	yeld
33	9.5.73	Corrour	71.4	49.0	44.0	8	yeld
34	25.5.73	Corrour	61.6	40.6	36.0	4	yeld
35	25.5.73	Corrour	65.2	43.8	39.6	5	yeld

1. Including the weight of the conceptus, but not that of some blood lost.
2. The estimated live weight of the hind, excluding the weight of the contents of the digestive tract and the gravid uterus
3. Empty-body weight, excluding the conceptus, rumen and lower digestive tract.

I was living and attending classes in Edinburgh over the period involved, and the stalker at one of the areas (Corrour) where most samples were obtained after the end of March, was by that time, engaged in estate work other than dealing with deer. Because of this it was not always possible to arrange mutually convenient days for going on the hill, and because the stalker was on holiday during April, these factors combined so that no hinds were collected during that month. However, a total of 19 hinds and their foetuses were collected, with an additional 10 foetuses having been collected during January, so that samples were collected over a period, and at a rate, sufficient for the objectives of this phase of the investigation.

2.2. Collection areas.

Ideally, all samples would have been collected from only one red deer population, or else sufficient numbers from different populations to enable tests to be made for differences that might exist between them. However, all estates approached showed reluctance to allow their deer to be shot out of season, and permission to do so was finally only obtained by agreeing to take only a small number from any one estate. It thus became necessary to take animals from different populations, at different times, in order to obtain samples over the whole of the proposed study period.

Animals were collected from the estates of Glen Feshie (10 hinds and 20 foetuses), Corrour (7 hinds and their foetuses) and Killilan (2 hinds and their foetuses). Glen Feshie is a privately-owned 'deer forest'[1] located in the southern

1 The use of the term 'deer forest' to describe an estate should not be taken to indicate that trees are necessarily present: the term means only that the estate is used mainly for the stalking of red deer for sport. Many of the deer forests of the Highlands of Scotland are almost exclusively rugged mountainous terrain, interspersed with blanket peat bog, totally devoid of any vegetation higher in stature than mature Calluna vulgaris.

Cairngorm mountains of the Badenoch district of the Highland region, and ranges in altitude from 320 metres (m.) to 1204m. The vegetation has been described in detail by Nicholson (1969); the low ground has remnants of the old Caledonian forest, (Pinus sylvestris and Betula species), and some juniper still exists. Poor quality Agrostis-Festuca is found in and near the flats through which the river Feshie runs, but the majority of the deer range is covered by Calluna-dominated vegetation.

Corrour is located about 40 kilometres (km.) southwest of Glen Feshie, on the eastern border of the Lochaber district of the Highland Region, and was privately owned as a deer forest until 1966. It is now owned by the Forestry Commission, and extensive planting of commercial forestry species has been carried out on the lower ground, which has been surrounded by a deer fence. The area from which hinds and foetuses were obtained ranges in altitude from 305m. to 1098m. The vegetation of the hill land is Calluna dominated, but somewhat larger areas of Agrostis-Festuca swards are present than are found at Glen Feshie.

Killilan is a privately-owned deer forest in the Loch Alsh district (Wester Ross) of the Highland Region. The major vegetation type is a grassy sward dominated by Molinia caerulea, Deschampsia flexuosa and species of Agrostis and Carex. The lowest ground normally inhabited by deer is around 61m. in altitude, while the highest is 898m.

The climate at Glen Feshie and Corrour approaches the continental type, with more frost and snow, less rain (particularly at Glen Feshie), and lower average temperatures than are normally experienced at Killilan: snow fell at Dalwhinnie, which is located between Glen Feshie and Corrour, on 44 days during the collection period of this phase of this study

(January to May, 1973); during the same period snow fell at Achnashellach, near Killilan, on only 28 days. Average monthly rainfall (based on data covering the years 1931-1960) over the period January-May at Dalwhinnie is 61 millimetres (mm.), while the equivalent average monthly figure for Achnashellach is 163mm. The average daily maximum temperature (also based on data from the years 1931-1960; see Meteorological Office, 1973) at Dalwhinnie ranges from a low of 2.7° Centigrade in January to 12.8°C. in May; the equivalent figures for Achnashellach are 6.0°C. and 14.7°C., respectively.

2.3. Collection procedure.

The foetuses and the hind that were collected prior to the 15th February (Table 2.1) were obtained during the normal taking of the culls at Glen Feshie and Corrour. The samples collected at Glen Feshie in March were taken in conjunction with an investigation being undertaken by personnel of what was then the Nature Conservancy (into variations in rumen protein levels, between the sexes and between different locations, over late winter; Dr. Brian Staines, pers. comm.). The samples from Corrour and Killilan taken after the 15th February were collected specifically for this project.

It has been traditional during the taking of the hind cull at Glen Feshie to select for yeld hinds[1], and hence all

1. Traditional practice on most if not all deer forests has been to attempt to select and shoot only yeld hinds during the taking of the hind cull. As tradition can be very strongly adhered to in some parts of the Highlands, and particularly by members of the professional stalker fraternity, the reasons given for this cannot be accepted without reservation. However, it is highly likely that the practice arose because the survival prospects of a calf which has lost its mother appear to be considerably lowered (the stated opinion of many stalkers is that they are virtually nil). Another possible reason for selecting for yeld hinds is that, as has been pointed out in the previous chapter, yeld hinds are likely to be heavier and in considerably better condition than are milk hinds. (It is unfortunate that this practice, while providing the best venison available, may have been, and still be, damaging the genetical potential of the deer herds subjected to it).

the foetuses collected there during the normal cull (i.e. those taken in January) came from yeld hinds. The investigation being undertaken by the Nature Conservancy required the shooting of both yeld and milk hinds, so some of the hinds collected at Glen Feshie during March were milk hinds. The sample ideally would have consisted of equal numbers of yeld and milk hinds being collected at each collection interval, but this was not possible because of the reluctance of proprietors or stalkers to allow milk hinds (or indeed, any hinds at all) to be shot out of season.[1] Because I was allowed to collect only two hinds per fortnight at Corrour, whether or not they were pregnant, I asked the stalker there to select yeld hinds (since over 90% of yeld hinds are normally pregnant, as compared to less than 50% of milk hinds; Mitchell et al., 1976, 1977). By May hinds could be visually recognised as pregnant, but, by chance, all the hinds shot that month were also yeld, and the sample population finally consisted of only four milk hinds. Only the very first hind shot (on 14th February) was not pregnant; it is because of this that the sample consisted of only 19 (rather than 20) hinds.

The collection procedure involved going out on the hill with a stalker and stalking deer in the traditional manner. The hinds were killed by shooting with a .243 Winchester or

1. The conservative, traditionalist natures of many stalkers can considerably inhibit the carrying out of scientific research on wild red deer in Scotland. For instance, although the stalkers, on one of the estates from which samples for this research were acquired, had been instructed by the proprietor to provide whatever animals were required (which in this instance necessitated the shooting of some milk hinds), because the stalkers disagreed, on principle, with shooting milk hinds, it 'just happened' that no milk hinds ever were within shooting range (!), and all the beasts shot were yeld. Occasionally my own research was frustrated: if I wanted something done with which a stalker disagreed, although he might say that he would do it, it somehow just never was done.

.270 Winchester (calibre of the cartridge) rifle. To minimise the damage done to body tissue, I requested that if possible the hinds be shot in the neck. This was rarely achieved at one area, but all the hinds from Corrour and Killilan were shot in the neck.

Hinds were bled within five minutes of shooting, by inserting a knife into the base of the neck, at the point where it joins the chest, and severing the jugular vein. Attempts were made to measure the out-flowing blood, initially using a measuring cylinder, and latterly by collecting in a bucket and weighing. However, the amounts of blood that were extractable varied considerably, depending on such factors as where in the body the bullet had entered, and the extent to which coagulation had already taken place (which varied according to how soon after death the animal was bled, and also appeared to vary with temperature of the air). Because the amounts of blood which could be taken from the animals was found to vary so considerably, and because with some of the animals the stalker bled them without collecting the blood (although he had been asked to do so), while I was removing the gut-intestinal tract and uterus, weight of blood lost is not included in the estimates made of the live weights of the hinds.

After bleeding, a hind was cut open and the gut-intestinal tract and gravid uterus removed (the process referred to as 'grallochíng'). The conceptus was dealt with as described later in this chapter. The rumens were weighed on removal from the bodies, and at Glen Feshie they were cut open so that samples of their contents could be obtained (for the research being carried out by the Nature Conservancy). On the last nine animals, measurements were also taken of

heart-girth and hock length. These were measured to the nearest 0.5 centimetres (cm) with a fibreglass tape, in the hope that the measurements could be related to the body weights and condition of the hinds. The heart-girth measurement was taken immediately behind the point where the forelegs join the body, at an angle perpendicular to the main body axis. The tape was checked to ensure that it was not twisted, and then pulled tight until all slack was taken up, but not so tight that the releasing of pressure on the ends of the tape caused the measurement to increase. It was originally planned to take girth measurements both before and after gralloching. However, it so often proved impossible to restrain the enthusiasm of the stalkers to get the gralloching over with and be off after more hinds, or home, that very few pre-gralloching measurements were made, and I finally abandoned the attempt to do so. The measurement of the hock (cannon bone) was made on the left leg, by bending the foot downwards, holding the cannon parallel to the main body axis and measuring from the distal to the proximal ends of the bone. The gralloch was then placed in a plastic bag, which was sealed and placed in a rucksack. The hind was then dragged by rope to the nearest point of access, for pick-up by vehicle or pony.

Foetuses were removed from the bodies of their dams within fifteen minutes of the death of the hind. In the last 16 samples the weight of the gravid uterus was recorded immediately upon removal from the body, and the volume of uterine fluids was measured in a graduated cylinder as the foetus was removed from the uterus. The umbilicus was cut approximately 2 cm. from the foetal body. Both foetus and uterus were then immersed in ethanol, which was carried in

a large vacuum flask ('Thermos' flask, model 82), to which chips of solid carbon dioxide ('dry ice') had been added. The mixture of alcohol and dry ice rapidly achieved an approximate temperature of -77° C., and the small foetuses (collected in January, February and March) froze almost immediately. By May the foetuses were too large to fit into the vacuum flasks available, and the freezing mixture was placed in the plastic inner bucket of a 'Racasan' chemical toilet (the bucket was approximately 0.66m. high). The lack of insulation of the container, with the subsequent raising of the temperature of the freezing mixture, was probably at least part of the reason that the foetuses collected in May took up to 25 minutes to freeze entirely. Once frozen, foetuses and uteruses were placed with an identification label in a plastic bag, and kept in the freezing mixture container until arrival at the larder. There they were placed on blocks of dry ice, in a large insulated wooden trunk, and transported to an electric blast freezer (with a temperature of -15°C.) within four to ten hours.

'Larder' weights (the weights of the bodies, less the gut-intestinal tracts, gravid uteruses and the blood that had been lost) were recorded for the hinds immediately on arrival at Glen Feshie or Killilan estate larders. The beasts from Corrour were taken directly to the Carcass Evaluation Unit of the East of Scotland College of Agriculture, at Bush Estate, Midlothian, and their larder weights recorded on arrival.

At Glen Feshie the lower jaws (mandibular bones) of the hinds were removed and kept by the Nature Conservancy. The kidneys and all associated fatty tissue were also removed and weighed, and the weights of kidneys alone were then taken. Trachea, heart, lungs, oesophagus and all internal organs

were removed in the larder and placed with the kidneys and associated fatty tissues in plastic bags. These bags and the unskinned carcasses remained in the larder at Glen Feshie for from 12 hours to five days. This was regrettable, but the lack of a freezer made the procedure unavoidable. At the time (March, 1973), the temperature of the air in the larder at Glen Feshie was below freezing during the nights, and for much of the daytime as well. The hinds collected at Corrour had only their grallochs and uteruses (with their contents) removed in the field, and were taken to the Caracass Evaluation Unit and placed directly into blast freezers (at -15°C.). The hinds from Killilan also had only their gut-intestinal tracts and conceptuses removed in the field. The first hind collected there (hind 30) remained in the estate larder overnight, and was taken with the next hind (hind 31) to a commercial cold storage facility at Conon Bridge, Rosshire, the following day. Both hinds were kept there (again at a temperature of -15°C.) for around a month, before being transported to the Carcass Evaluation Unit by Landrover. Both hinds appeared to be still frozen at the end of this transfer.

2.4. Difficulties encountered during the collection procedure.

The first and major difficulty encountered, while collecting hinds and foetuses for this research, was in obtaining the permission of estates to carry out research on their deer. It was then necessary to gain (as much as possible) the co-operation of the stalker(s) involved. While little other than indifference was shown during the normal stalking season, in some cases a level of passive resistance was encountered when collecting after the 15th of February, and considerable diplomacy was required to obtain the hind and foetus samples in the manner required. Even after a working relationship

had been established, stalkers were almost always keen, having shot and gralloched one or more hinds, to get on after more deer, or to go home. Since my presence was on sufferance, such an attitude sometimes required the curtailing of measurements taken in the field, to avoid jeopardising the relationship of cooperation that had been established. (It is usually advisable that, in such situations, only the minimum of essential measurements be carried out while in the field).

The equipment needed for the collection of the samples taken in the field was carried in a large stout rucksack. Before going out on the hill a quantity of ethanol was poured into a vacuum flask, which was placed in the rucksack. Since the efficiency of the freezing mixture decreased rapidly after around half an hour, the dry ice was carried separately, and not added to the flask until a sample had been procured. Furthermore, since dry ice rapidly evaporates when in small pieces, it was carried in approximately 2 kilogram (kg) blocks (wrapped in the heavy paper in which it was purchased), and a geological hammer was also carried to break it, when required, into the small pieces needed to produce the freezing mixture rapidly. Dry ice can produce severe burns if it comes in contact with bare skin, and waterproof gloves therefore were used to handle it. Ordinary wooden laundry tongs, still obtainable from some ironmongers, were used to retrieve samples from the freezing mixture.

Care was required to ensure that the gas release valve on the lid of the vacuum flask did not become clogged while the flask contained the freezing mixture. This situation occurred with one of the sampled foetuses (the 13th to be collected!), and the build-up of pressure within the flask caused an explosion which shattered the glass lining of the

flask. Although replacements are available, they are too fragile to carry unless in the flask, and I therefore lost the opportunity (which existed that day) of collecting several more foetuses.

The gastro-intestinal tracts of shot deer had to be placed in the rucksack and carried, in addition to the paraphernalia used to freeze the foetuses, and this placed a restriction on the number of samples that could be collected in any one excursion. One day at Glen Feshie I collected three foetuses in an afternoon, and ended up having to carry my equipment, the intestinal tracts and conceptuses of the three hinds, and furthermore had to drag the body of a shot calf as well. Fortunately, the majority of the approximately 2 km. to be travelled was down-hill. On reaching the larder, the rucksack was weighed and found to be around 36 kg. (80 lbs). (Thus work of this type can be rather strenuous, and ought not to be undertaken lightly).

Age estimation of the collected hinds.

The hinds collected at Glen Feshie had had their lower jaws (mandible bones) removed and kept by the Nature Conservancy, for ageing purposes; the ages of these hinds (see Table 2.1) were provided by Dr. Brian Staines. The age of the hinds from Killilan and Corrour were estimated by A.B. Cooper, Esq., after the method of Mitchell (1967): whereby the lower first molar was removed, cut in section, the resulting exposed surfaces ground smooth with sandpaper, and cement layers counted under a dissecting microscope. The accuracy of this method of age estimation is not exact, and it is possible that the age of some of the collected hinds has been estimated incorrectly: however, this error should not be greater than $\pm$ 1 year.

2.5. Dissection procedure.

As stated in the previous section, all hinds had their larder weights taken soon after shooting, and sooner or later were transported to the Carcass Evaluation Unit and placed into storage in a blast freezer. At the time, several dissection investigations were being carried out at the Unit, with varying degrees of priority. The collected hinds therefore were dissected as and when time was available. In some cases a backlog of animals to be dissected built up, and because I had not given sufficient thought to the matter, the hinds were not all dissected in the same order as they had been collected. The lengths of time they spent in storage therefore varied, as shown in Table 2.2.

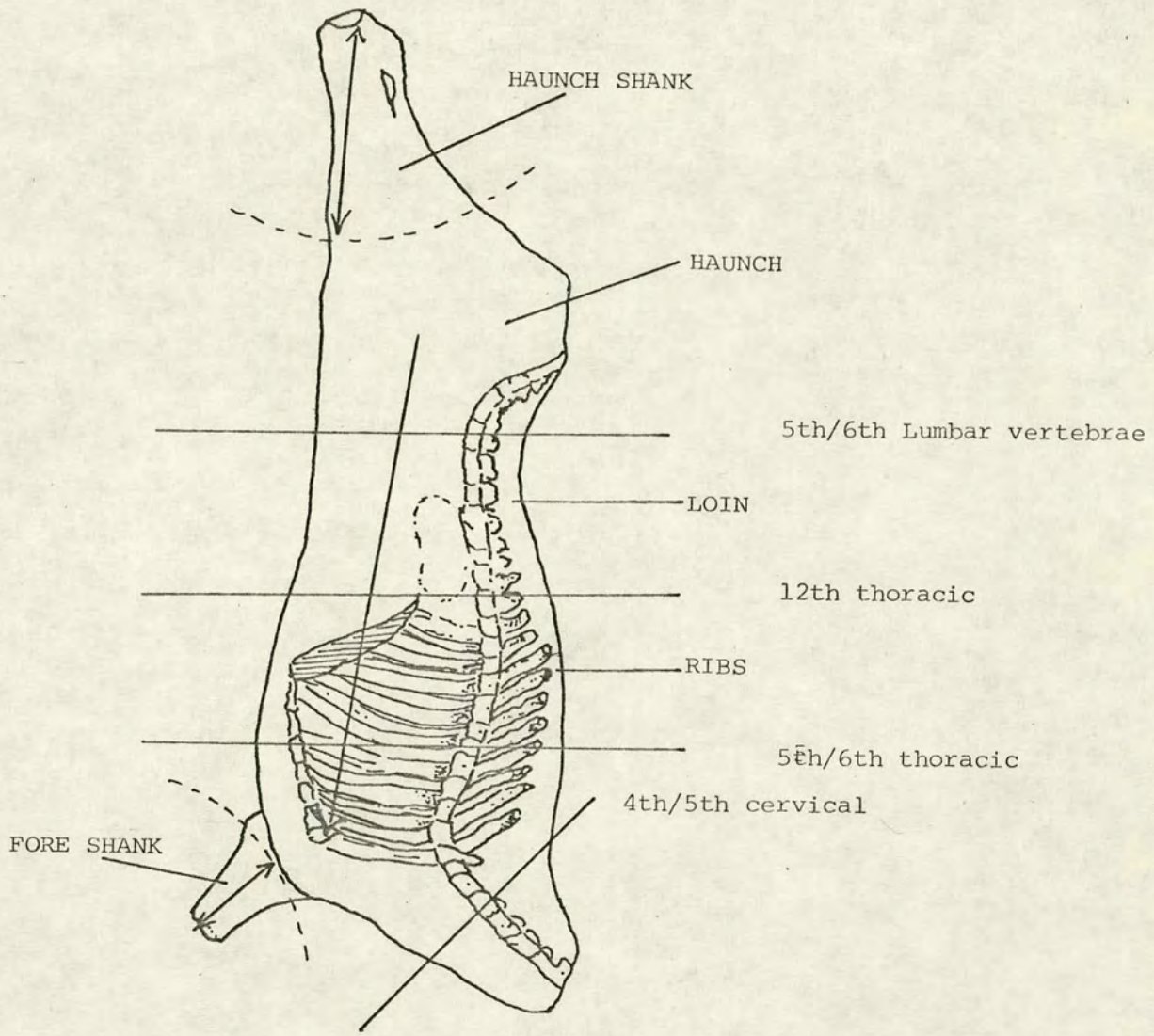
The average length of time the bodies of the hinds remained in storage was 128 days, but it can be seen that some were dissected much sooner than this (e.g. hinds 18 and 19) and others considerably later (e.g. hinds 25-28). Unfortunately, the carcasses were not weighed immediately on removal from storage (due to a misunderstanding), so that the weight lost due to evaporation during storage cannot be known. Summation of the weights of the body components after dissection shows that the bodies, less intestinal tracts and conceptuses, underwent an average weight loss of around 9% during storage and preliminary dissection (into pelt, head, internal organs and 'cold carcass').

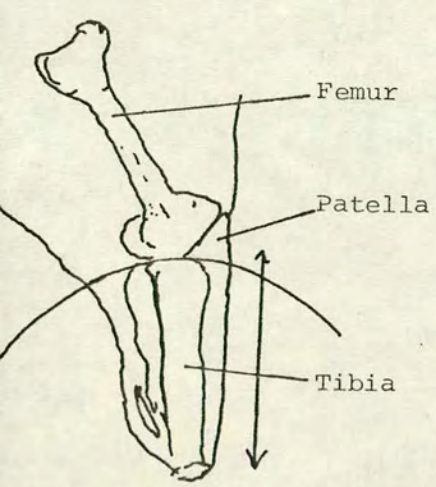
The dissection procedure entailed removing a carcass from the freezer and allowing it to thaw (usually overnight) until skinning was possible. The hocks were first removed, by cutting at the distal end of the fibula or ulna. The head was removed by cutting between the atlas and the axis, the

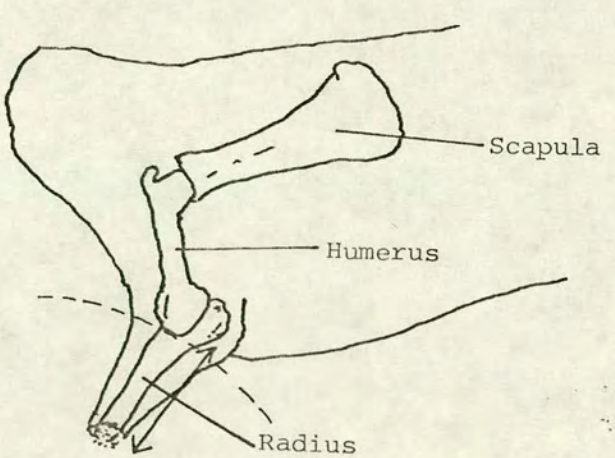
Table 2.2: the number of days the hind samples spent in cold storage.

hind number	date shot	date dissected	days in storage
17	14 February 73	7 November 73	270
18	7 March 73	19 March 73	12
19	7 March 73	18 March 73	11
20	26 March 73	2 May 73	37
21	26 March 73	29 May 73	64
22	26 March 73	15 May 73	50
23	28 March 73	4 May 73	37
24	28 March 73	14 May 73	47
25	28 March 73	29 October 73	215
26	28 March 73	6 November 73	223
27	29 March 73	6 November 73	222
28	30 March 73	2 November 73	217
29	30 March 73	28 May 73	59
30	3 May 73	29 October 73	179
31	4 May 73	22 October 73	171
32	9 May 73	24 September 73	138
33	9 May 73	24 October 73	168
34	25 May 73	29 August 73	96
35	25 May 73	22 October 73	150

Figure 2.1. showing the positions at which cuts were made to divide the half carcass into the major joints, and these joints.







atlas remaining with the skull. The carcass was then skinned, weighed, and aplit into its two halves by cutting down the spinal column by hand or using an electric band saw. Time was not available to carry out dissection of both sides of the carcass, and all further dissection therefore was carried out on one side only. In all but two of the hinds, the left side was dissected. The left shoulders of hinds 27 and 28 had been badly damaged by the rifle slugs, so the right sides of these two hinds were dissected instead. Except where stated otherwise, the word carcass will be used henceforth to mean only one side, the 'butcher's half carcass'.

The half carcass was initially divided into four major parts, corresponding to the butcher's major wholesale joints of the gigot (hind leg), shoulder and neck, rib and loin, and the weight of each joint was recorded. The gigot joint was removed by a cut made at right angles to the vertibral column, crowding the anterior end of the tubercoxae. The shoulder joint was removed by cutting between the fifth and sixth ribs, crowding the sixth rib, and carrying the line of the cut on to the dorsal and ventral edges. The loin and ribs joints were made by splitting at the twelfth and thirteenth ribs, the knife crowding the twelfth rib. (The basic dissection procedure, and the resulting joints, are shown in Figure 2.1).

The fold of the flank was removed by cutting at its point of attachment to the rest of the carcass. The shank of the gigot was removed by inserting a pin at the distal end of the tibia, measuring the distance from there to the patella, and then using this distance to circumscribe a line around the joint and cut away the shank (see Figure 2.1). The remainder of the gigot, or haunch, was regarded as the

'prime' cut.

The brisket and flank joints were removed by a cut made along a line drawn from the point at the base of the first rib to the base of the thirteenth, and projecting this line back across the loin. This line was marked with a knife before jointing. The loin and rib flanks were classified as secondary cuts of these joints. The fore shank was removed by inserting a pin at the distal end of the radius and measuring the distance to the distal end of the humerus, and then cutting away the shank.

The brisket and fore shank were classified as secondary cuts of the shoulder joint, as was the neck. The neck was removed by taking a cut in line with the thoracic vertebrae at a point one-third of the distance of the third cervical vertabra from the anterior edge. The remainder of the shoulder was classified as the prime joint.

All primary and secondary joints were weighed and then dissected into; sub-cutaneous fatty tissue, intermuscular or associated fatty tissue, muscle, and bone, and these tissues were weighed. While any one joint was being dissected, the remainder were kept wrapped in damp towels to try to reduce moisture loss. This completed the dissection procedure and the collection of physical data.

2.6. Preparation for chemical analysis.

After dissection the components of the half carcass and the head, pelt, lower legs and internal organs were grouped together in five groups as follows:

Group 1: the muscle, fat and bone tissues of the haunch shank joint;

Group 2: the tissues of the shoulder shank joint;

Group 3: the tissues of the shoulder prime, brisket and neck joints;

Group 4: the tissues of the haunch prime, flank, ribs and loin joints; and

Group 5: the remainder of the body (head, pelt, hocks, and internal organs).

(Unfortunately, the uteruses were included in Group 5 and were not analysed separately).

The muscle and bone tissues of Groups 1 to 4 were placed (by tissue) in a Wolf-King soft-tissue mincing machine and ground, using progressively smaller plates with holes from 10mm to 2.5mm in diameter. This process was then repeated, resulting, with the muscle tissues, in homogeneous samples.

Fat tissues were when possible minced to achieve homogeneity in a small bench grinder, but this was not possible when the dissected tissue consisted of less than about ten grammes (g). The remainder of the body (Group 5) was submitted to the same progressive mincing process as the muscle and fat tissues to obtain a relatively homogeneous sample; small chips of bone (of up to 2.5mm in diameter) and much of the hair of the pelt remained discrete, but were evenly distributed throughout the sample material. After mincing, all samples were placed in air-tight plastic containers, labelled and frozen.

At the end of dissection and mincing, there were approximately 320 discrete samples of the three main tissues from different parts of the bodies of the 19 collected hinds. Neither the time nor money was available to perform chemical determinations on every one of these samples. Instead, samples representative of the whole empty (ingesta- and conceptus-free) bodies of the hinds were reconstituted from the

samples of the various body components. This involved taking a sub-sample from each tissue, from each of the five Groups, of a weight (in g) which was equivalent to the percentage the particular tissue represented of the whole empty body. Combining these sub-samples resulted in a reconstituted sample of around 100g, which was representative of the entire empty body of the hind. The sub-samples of the different tissues, from the different areas of the body, were taken using a quartering method: each sub-sample was progressively quartered in a dissection tray, by a clean spatula, until a sub-sample of the appropriate weight remained.

Once prepared, the 100g representative samples were taken to the Central Analytical Laboratory of the East of Scotland College of Agriculture. There they were processed and chemical determinations of their contents made as described in section 2.7.

The 29 foetuses which had been collected were dissected, and their internal organs weighed, as described by Anderson and MacDonald (in press). After dissection, the entire foetus was ground in an ordinary bench mincing machine (using a plate with holes of 1.5mm diameter) to achieve a single homogeneous sample. Using the quartering method, a sub-sample of around 100g was then taken, put into a plastic container, labelled and taken to the Central Analytical Laboratory. The remainder of the foetuses were bagged, labelled and refrozen.

2.7. Chemical determination.

2.7.1. Determinations made on the hind empty-body representative samples and on the foetal sub-samples.

Both the sub-samples of the foetuses and the 100g samples (representative of the entire empty bodies of the hinds) were

analysed to determine their

dry matter (DM) content (percent);
gross energy content (in kcal/g DM);
chemically-determinable fat content (percent in DM);
nitrogen content " ;
phosphorus content " ;
sodium content " ;
potassium content " ;
calcium content " ; and
magnesium content.

On arrival at the C.A.L. the samples were immediately freeze-dried to stop the possible separation of fat. During this process the DM contents of the samples were determined. Homogeneity was achieved by the samples being ground in a high speed, ultra-centrifugal mill, the sample material being forced through a sieve of approximately 1mm diameter.

Gross energy content was determined by combustion of a portion of each sample in an adiabatic bomb calorimeter.

Chemical fat was determined in a Soxhlet apparatus using petroleum spirit (at 40° to 60°C), extraction taking place for a period of five hours.

After Kjeldahl digestion, nitrogen content was determined colorimetrically using the process of Crooke and Simpson (1971).

Phosphorus content was determined colorimetrically by the procedure of O'Neill and Webb (1970).

Sodium and potassium contents were determined by emission spectroscopy.

Calcium and magnesium contents were determined in an atomic absorption spectrometer, lanthanum being used to eliminate the interference of phosphorus.

2.7.2. Further determinations made on the tissues of six selected hinds.

In addition to the determinations made on the whole

empty-body representative samples of all the hinds, the DM, ash, nitrogen and fat contents of the muscle, bone and fat tissues from the five body Groups were made for six selected hinds (see Chapter 3, section 3.2). The DM, nitrogen and fat contents of these tissue samples were determined in the manner described in section 2.7.1. Ash content was determined by overnight ignition in a muffle furnace, at 500°C.

2.8. The representativeness of the collected hind sample.

The purpose of this part of this research was to establish why wild Scottish red deer hinds experience the losses in body weight which they regularly do over the winter and spring months. The hypothesis was proposed in Chapter 1 that the major reason for this weight loss is because hinds are in a state of negative energy balance during part or all of this period (as a result of an insufficient supply of dietary energy then being available to them, while high environmental demand, and, in pregnant animals, the demands of the developing foetuses, also are occurring). This hypothesis was to be tested by examining how the energy content of the 19 hinds might vary over the collection period 14 February to the 25th May. The second objective was to analyse the changes which might be occurring in the physical and chemical composition of the bodies of the collected hinds, in relation to any change found in energy content, so as to try to establish the reasons for such changes, their magnitudes, and rates and duration of occurrence.

It was intended that the sample population of 19 hinds should be representative of the wild populations from which they were taken, so that changes found occurring in them could be assumed to be similar to and indicative of what is

happening to the majority of wild Scottish hinds over the period February to June. However, the magnitude of the energy deficit experienced by hinds, and hence the physiological effects caused by this deficit, can be expected to vary between and even within populations. Variation in the degree of energy deficit experienced can arise between populations due to differences in the dietary energy available from vegetative resources; either because of differences in herbage quality, or in availability (depending upon population density). As mentioned in section 2.2, variation may also exist in environmental energy demand, depending on the severity of the weather, and the amounts of cover available between areas. It can also arise within any particular area between years, due to weather differences. Within a given deer population, the energy deficiency experienced by individual animals can vary according to state of dentition, and the ages and body sizes of hinds, if these characteristics give rise to differing metabolic requirements. Variation can also arise within a herd, depending on the lactational and reproductive status of individual hinds.

The many possible sources of variation in the magnitude of the energy deficit suffered by individual hinds during the winter mean that no single figure can be proposed to accurately describe all of them. To be able to do so would require studies being made into every age, reproductive and lactational class, in every herd, in every part of the country. It therefore seems justified to try to establish a figure which can be used to calculate a rough average value for the winter daily energy requirements of the majority of pregnant adult Scottish hinds, from any area. Therefore, the fact that the hind sample population collected for this

research were of different ages and lactational states, and came from differing areas of the Highlands, tended to suit this purpose.

The sample population of 19 hinds included only four milk hinds. Since milk hinds tend to be poorer in condition than yeld hinds (Mitchell et al., 1976, 1977), it seems likely that milk hinds are normally subjected to a greater energy deficit than are yeld animals, due to the energetic cost of lactation. However, Mitchell et al. (1976) had difficulty in deciding if some hinds which they had collected in late winter or spring were milk hinds; some animals which seemed to have calves with them, had very little or no milk in their mammary glands. Although such a situation can arise due to an orphaned calf adopting another hind to follow, it possibly also is an indication that some hinds have ceased to lactate by March or April. These hinds therefore presumably would not be suffering as great a daily energy deficit as the majority of yeld hinds at this time (since the energy demand of lactation will have ceased, and the probability is greater than 50% that they are not pregnant). Thus the energy requirements of yeld hinds may be less than those of most milk hinds in early winter (since the energy demand of the foetus has not yet become large), but become greater than those of milk hinds by March or April when 'milk' hinds may have ceased to lactate, and yeld hinds are having to provide daily increasing amounts of energy to the products of conception). Such a hypothesis could explain why it is that yeld and milk hinds tend to be most similar in body weight and condition at the end of the winter (Mitchell et al., 1976). It may therefore be the case that estimates of daily energy requirements which are derived from the 19 hinds of the present study will

tend to underestimate the requirements of milk hinds in February, and somewhat overestimate them as summer approaches.

The average age of the sample population was 6.7 years (including one hind as young as 4, and one as old as 10 years), and therefore well represents 'adult' (4 to 10 year old) animals (although not including animals of each age from each interval of the collection period). The majority of the hinds in the sample was collected from areas of relatively severe winter weather (Glen Feshie and Corrour), and the average energy deficit experienced by them therefore may be somewhat higher than that experienced by hinds from areas with a more moderate climate (e.g., the Western Highlands). However, the deficit indicated by the sample population is probably similar to, or even slightly less than that experienced by deer in the Northern Highlands (northern Ross-shire, Caithness and Sutherland).

As pointed out in section 2.3, hinds were not collected strictly at random from Killilan and Corrour, since the constraints placed upon the numbers of animals that could be collected made it imperative that all the hinds that were shot were pregnant. Therefore the first three hinds collected (hinds 17 to 19, from Corrour) were selected because they were yeld hinds, because of the considerably higher probability of yeld hinds being pregnant (Mitchell, 1973; Mitchell and Brown, 1974; Mitchell et al., 1976, 1977; the last named authors reported finding 93% of yeld hinds pregnant, as compared to only 43% of milk hinds). The hinds at Glen Feshie were being shot as a random sample of equal numbers of both yeld and milk hinds, and I therefore was able to collect the foetus and body of any hind shot when I was present; this resulted in the collection of 6 yeld and 4 milk hinds, and

their foetuses, from a larger random sample. By May it was possible to distinguish pregnant hinds visually, and selection of the last six hinds of the sample (hinds 30 and 31 from Killilan, and 32 to 35 from Corrour) was made simply on this basis: fortuitously, all six were found to be yeld animals.

Excepting the points just discussed in this section, there is no reason to believe that the 19 hinds or the dams of the first 10 foetuses collected are not a random sample of the hind populations within the three collection areas. It therefore appears to be acceptable to assume that as a sample population they are typically representative of these populations. The sample was too small for testing for differences between areas, but because of the relative similarities in climate and vegetation between Glen Feshie and Corrour, it is assumed that the hinds in these two areas normally are exposed to similar energy regimes. The two hinds collected from Killilan are included in the sample because they were found to have gross energy contents which mathematically lay between those of the two hinds collected a week later at Corrour (see Chapter 3, Table 3.1 and Figure 3.1).

In view of the lack of evidence to the contrary, the 19 hind sample collected for this study appears to be as reasonably typical of the majority of adult, wild, pregnant Highland deer as could be achieved, without taking such a much larger sample that it would not have been possible, for temporal and financial reasons, to carry out the study. It therefore seems legitimate to assume that the physiological processes observed in the sample to be occurring over the period February to June (and particularly changes in energy status) are similar to those occurring in the majority of wild hinds.

2.9. Some comments on the collection and analytical procedures.

The shooting of the collected hinds was done by stalkers employed on the various estates. All field collecting and recording was done by myself, or supervised in my presence. The dissection and mincing of the bodies of the hinds was done almost entirely by J. Fraser, Esq., of the Carcass Evaluation Unit; I assisted with the dissection and mincing of only some of the hinds. This was because, at the time, I was engaged in attending classes, or, after the end of March, 1973 was living in Ross-shire, preparing for an experimental feeding of wild hinds. It would have been much preferable if I had nonetheless assisted with most, if not all, of the dissections (although my presence would have been of little assistance to the considerable expertise of Mr. Fraser). The dissection and mincing of the foetuses were done by A. MacDonald, Ph.D., and myself (Anderson and MacDonald, in press). The preparation of 100g. samples for chemical analysis was done entirely by myself. The chemical determinations were carried out by Dr. P. Crooks and the staff of the Central Analytical Laboratory.

As this study progressed it became obvious that I had not always given sufficient thought to the matter of what had to be done to achieve the research aims. Thus I should have ensured that the bodies of the hinds were dissected in the same order in which they had been collected, and that they were weighed on removal from storage, so that the moisture loss which had occurred could be established precisely. I also should have kept samples of uterine fluids, so that the energy contents of them could be determined, and ensured that the uteruses themselves were analysed as discrete samples, instead of allowing them to be minced with the remainder of

the parts of the body (in Group 5). Furthermore, it now is apparent that the muscle (and bone and fat) tissue of the upper haunch, loin and ribs should not have been combined and minced as a single sample, but rather kept separate (i.e. samples should have been prepared of the muscle of the upper haunch, of the loin, and of the ribs separately, rather than lumping them all together in Group 4), since the effects of undernutrition appear to be different in the haunch than in the loin and the ribs. The problems which arose from having proceeded in the ways mentioned (or from not having done so) are discussed in the appropriate sections of subsequent chapters.

The determinations of the DM, nitrogen, ash and fat contents of the muscle, bone and fatty tissues from each area of the bodies of six chosen hinds was intended to be a pilot study to establish where within the body changes of particular interest might have been occurring; once such changes had been identified, they were to be examined by determinations of the appropriate tissues being made from all 19 hinds. Unfortunately, the large walk-in freezer in the Department of Forestry and Natural Resources of Edinburgh University (where the samples were in storage) broke down while these initial determinations were being made. The break-down occurred over a weekend, and the alarm bell fitted to the freezer and intended to sound should the temperature rise above freezing, also malfunctioned, so that the break-down was not discovered until late the following Monday. By this time, the majority of the samples of the tissues of the hinds, and the foetus. samples had completely thawed and begun to decompose. It therefore was not possible to carry out any further determinations..

CHAPTER 3. Changes in the Chemical Composition of the Bodies of the Collected Hinds.

The considerable loss in body weight, which most (if not all) wild red deer hinds undergo during winter and spring, is one of the most obvious features of the low productivity of the species in Scotland. In Chapter 1 of this thesis I suggested that the major reason for this weight loss is because hinds are in a state of negative energy balance for most if not all of the period during which it occurs. To test this hypothesis, 100g composite samples were prepared (as described in the previous chapter) to represent the empty bodies of the 19 collected hinds. ("Empty body" henceforth is used to mean the entire body of the live animal, excepting the contents of the gastro-intestinal tract, and of the gravid uterus). Determinations were made on these samples, so that changes in the chemical composition and energy content of the bodies of the collected hinds could be investigated. Observed changes have been submitted to simple linear regression and correlation analysis (in relation to time, as explained in the last chapter), to establish which of them are statistically significant trends. The results of these analyses are presented in this chapter, and then their possible implications (of physiological change occurring in the majority of wild Scottish hinds over the period mid-February to the end of May) are discussed.

3.1. Chemical changes in the composition of the representative samples.

3.1.1 ENERGY CONTENT.

The gross energy content of the 100g. samples representative of the empty bodies of the collected hinds, was found to drop from 5.8 kilocalories (kcal) per g dry matter (DM)

to around 4.8 kcal. per g DM over the 100-day collection period (Table 3.1; Figure 3.1). Statistical analysis shows that this decrease is very significantly negatively correlated with the passage of time ($r = -0.81$, $P < 0.001$).

3.1.2. DRY MATTER CONTENT.

The fall in gross energy content of the representative samples was accompanied by a drop in the dry matter content of the samples (Table 3.1). The fact that water losses from the bodies of the hinds occurred, during collection and storage (unavoidably; see last chapter), means that the figures presented for the other constituents of the body, as chemically determined, are not perfectly accurate descriptions of the actual quantities of these materials in the bodies of the live hinds. Because the DM percentages of the representative samples are higher than the real DM content, the figures given are overestimates of the actual quantities present in the living animals. The differences between the weights taken soon after shooting and those taken after storage and dissection (and taking account of the further losses which will have occurred during mincing and preparation for chemical analysis), suggest that this error is in the region of 8 percent of empty-body weight. The amount of moisture lost through evaporation could have been estimated by weighing the various carcass components before and after each stage in the preparatory process, but it still would not have been possible to know precisely how much of the weight loss observed was due to tissue destruction rather than evaporation, and no attempt has been made to correct the DM contents as chemically determined. It must therefore be borne in mind that figures given for the com-

Table 3.1: Energy and major chemical composition of the hinds.

HIND NUMBER	SAMPLE DRY MATTER (% in D.M.)	ENERGY KCAL/G DM	SAMPLE NITROGEN (% in D.M.)	FAT CONTENT (% in D.M.)
17.0000	41.6000	5.8234	8.0730	28.6800
18.0000	36.7000	5.7539	9.5700	22.7600
19.0000	38.7000	5.6862	8.7670	24.6000
20.0000	35.1000	5.4619	10.0330	19.7200
21.0000	38.1000	5.6840	9.2760	23.7200
22.0000	37.0000	5.6314	8.6910	23.4400
23.0000	36.2000	4.8834	11.0040	13.0400
24.0000	38.5000	5.4204	9.5700	21.5200
25.0000	41.0000	5.6651	9.1420	22.7200
26.0000	38.1000	5.6195	9.7820	20.2800
27.0000	39.1000	5.4984	9.5810	19.6800
28.0000	39.7000	5.4379	8.9230	19.3600
29.0000	36.7000	5.7409	8.9080	21.6400
30.0000	34.3000	5.0130	9.6340	12.4400
31.0000	33.2000	5.2537	10.7820	16.0000
32.0000	33.4000	5.3686	10.3670	11.5600
33.0000	31.6000	5.0006	10.3680	7.4000
34.0000	33.1000	4.8502	9.9400	7.1200
35.0000	32.2000	4.8927	10.5530	5.8800

GO :

Table 3.2: Mineral contents of the samples representative of the empty bodies of the collected hinds.

CALCIUM % IN D.M.	PHOSPHORUS % IN D.M.	MAGNESIUM % IN D.M.	SODIUM % IN D.M.	POTASSIUM % IN D.M.
5.6510	2.9890	0.1550	0.4410	0.7030
4.5740	2.5480	0.1430	0.4900	0.9640
5.3030	2.7800	0.1450	0.4540	0.8360
4.6890	2.5710	0.1340	0.4620	0.8710
5.2080	2.8010	0.1430	0.4280	0.8280
4.4690	2.4360	0.1290	0.4160	0.7820
6.6960	2.4550	0.1820	0.6090	0.8830
6.1640	3.2180	0.1610	0.5220	0.7240
4.9350	2.4450	0.1420	0.4410	0.7580
4.3750	2.3210	0.1410	0.4460	0.8500
5.0900	2.7720	0.1440	0.3490	0.8780
5.3520	2.7430	0.1480	0.3580	0.7530
3.6520	1.9810	0.1230	0.3430	0.7100
6.8820	3.0000	0.1940	0.4270	0.7240
4.8380	2.7350	0.1600	0.4300	0.8350
4.6150	2.6890	0.1560	0.4010	0.7730
5.2910	2.8280	0.1470	0.4380	0.8330
6.4080	3.2230	0.1820	0.4510	0.8170
5.7090	3.0550	0.1780	0.4170	0.8890

GO :

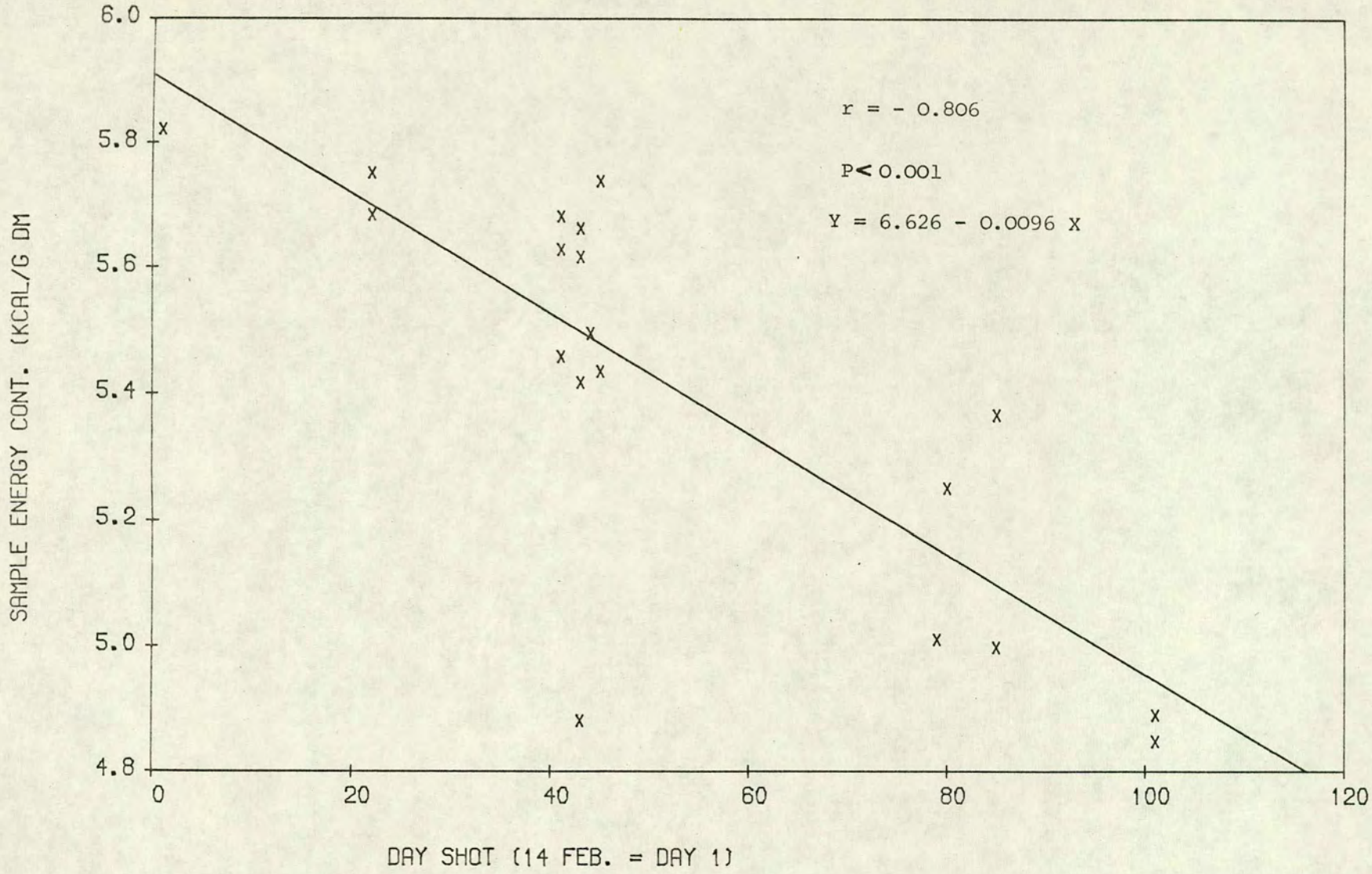


FIG. 3.1. DROP IN E-B SAMPLE ENERGY CONTENT

position of the whole empty body are slight overestimates.

Not only did the carcass samples unavoidably lose moisture during storage, examination and preparation for chemical analysis, but the amounts lost presumably vary between them, due to differences in the lengths of time they were stored before dissection. The last nine hinds collected remained in storage an average of 59 days longer than the first 10, and therefore their moisture losses presumably were greater. It is of interest that, nevertheless, a considerable drop in the DM content of the representative samples occurs over the sample period (Figure 3.2). Regression analysis suggests that the percent DM in the samples dropped at a rate of around 0.1% per day over the 100 days of the collection period; the real increase in the percentage of empty body weight which is water was presumably somewhat greater than this. However, it appears that it would be incorrect to overestimate the importance of the error in dry matter content introduced through variation in the length of time the bodies of the hinds remained in storage. Testing by correlation analysis showed that there was virtually no correlation between variation in dry matter content and number of days spent in storage ($r = 0.198$, $t = 0.836$, $P = 50\%$), in contrast to the correlation between dry matter content and the date the hinds were shot ($r = -0.845$, $P < 0.001$; see Figure 3.2).

3.1.3. FAT CONTENT.

The fall in gross energy and DM content in the representative samples was also accompanied by a drop in the amount of fat present (Table 3.1). The percentage of the DM that was fat fell from around 28% to less than 8%. In terms of live animals, the hind collected in mid-February contained

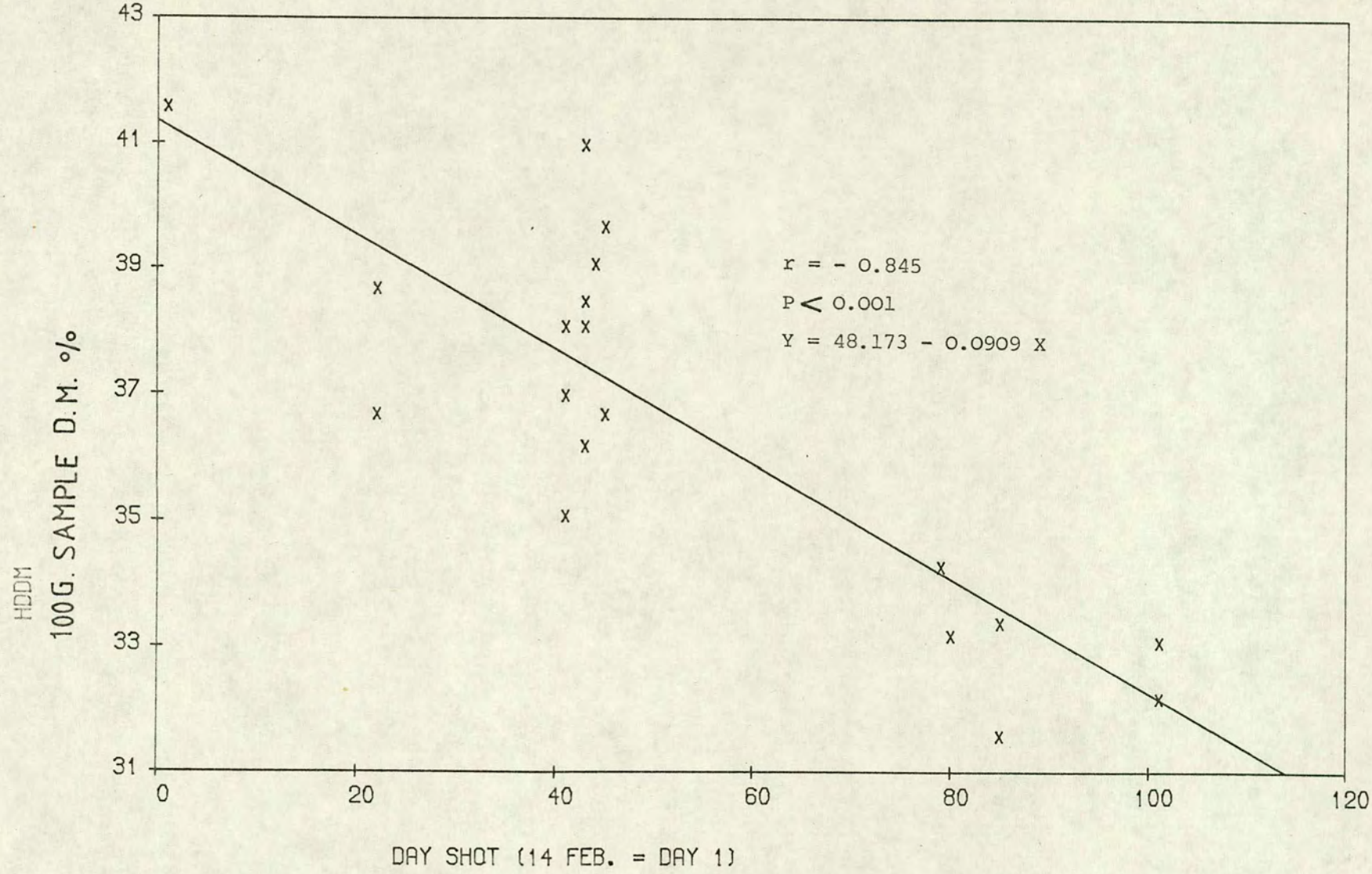


FIG. 3.2. DROP IN E-B SAMPLE DRY MATTER CONTENT

around 6.5 kg of fat in her body. In comparison, the two hinds collected at the end of May contained an average of only around 860g. Regression analysis of the entire sample estimates that the percentage of the empty body weight that is fat decreased from around 11% to only 2% (Figure 3.3).

3.1.4. NITROGEN CONTENT.

The percentage of nitrogen in the DM of the representative samples increased significantly over the collection period (Table 3.1). This increase is presumably the result of the progressive decrease in the percentage of fat in the DM. The weight of protein present in the samples, as estimated by multiplying the weight of nitrogen present by 6.25 (MacDonald et al., 1973), appears to have dropped over the collection period, although the decrease was not statistically significant ($r = -0.25$, $P > 0.1$).

3.1.5. MINERAL CONTENT.

The amounts of the major mineral nutrients present in the representative samples are given in Table 3.2., expressed as percentages of the DM. The average percentage of phosphorus in the samples was 2.67%. Percent phosphorus increased slightly over the collection period, but the increase, at least with the present sample size, was not significant ($r = 0.38$, $P > 0.1$). The average sodium content of the representative samples was 0.438% of the DM: the minimum value was 0.343% (hind no. 29); the maximum, 0.609% (hind no. 23). No statistically significant correlation was found between the percent sodium in the DM of the samples and the date when the hinds they represented were shot. Average potassium percent in the DM of the samples was 0.81%, with

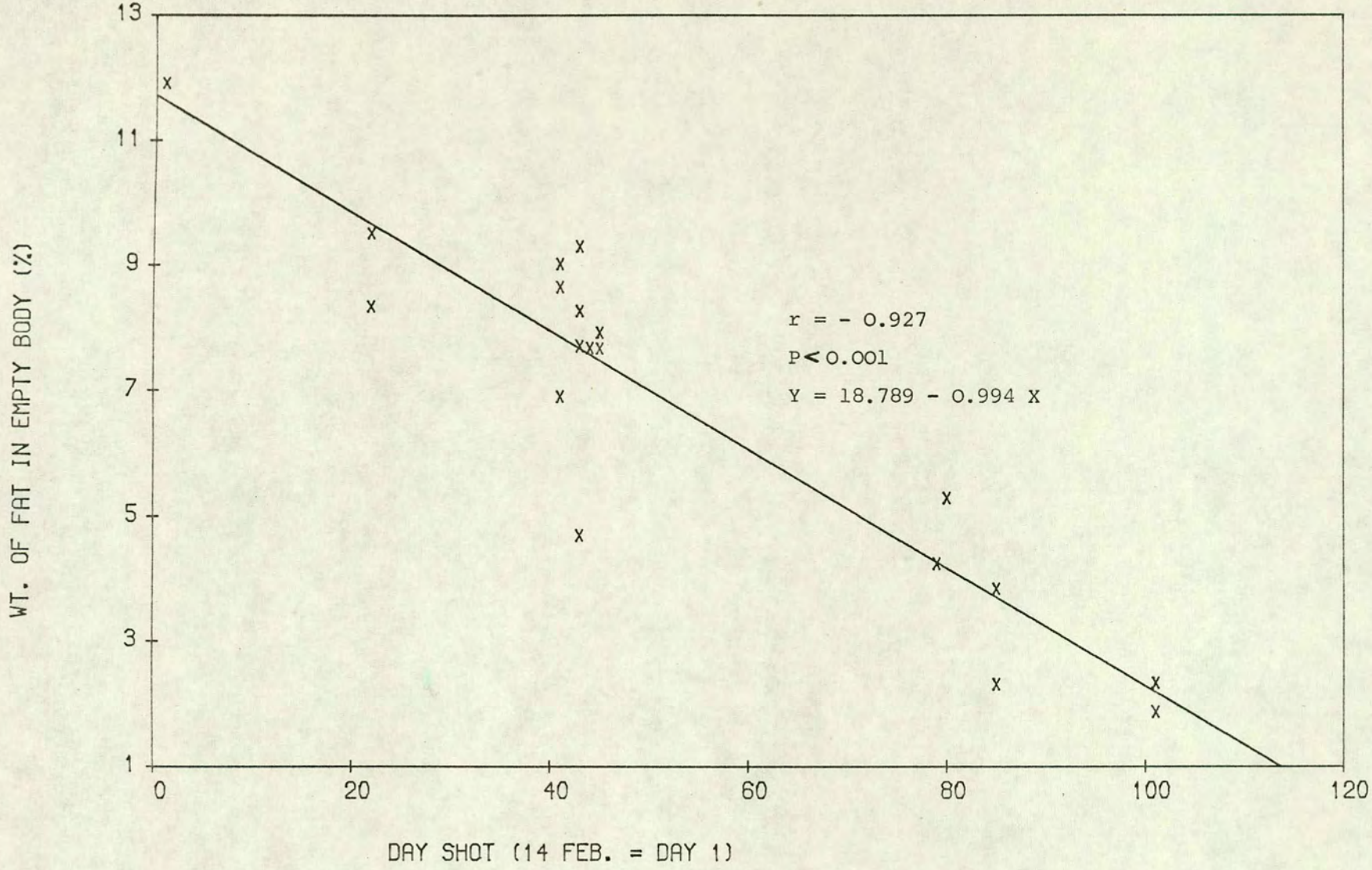


FIG. 3.3. DROP IN % FAT IN EMPTY-BODY WT.

a minimum value of 0.703% (hind no. 17), and a maximum of 0.964% (hind no. 18). Again, no significant correlation was found between percent potassium in the samples and time. Average percent calcium in the DM of the samples was 5.258%, with a minimum of 3.652% for hind no. 29, and a maximum of 6.882% for hind no. 30. There was a slight, but statistically non-significant increase in the percent calcium in the samples as time progressed ($r = 0.26$, $P > 0.1$). The average magnesium content of the samples was 0.153% in the DM, with a minimum value of 0.123% (hind no. 29), and a maximum of 0.194% (hind no. 30). The percent magnesium in the DM of the samples increased significantly over the collection period ($r = 0.53$, $P < 0.02$; see Figure 3.4).

3.2. Changes in the percentages of DM, ash, nitrogen and fat in specific tissues.

In addition to the determinations made on the representative samples of the whole empty body, the DM, ash, nitrogen and fat contents of muscle, bone and fat tissues located in different parts of the half carcass were determined in six of the carcasses from the hind sample. The hinds investigated in this manner were no..17 (shot on 14.2.73), no. 20 (shot on 26.3.73), no. 24 (shot on 28.3.73), no. 30 (shot on 3.5.73), no. 32 (shot on 9.5.73) and no. 35 (shot on 25.5.73). Thus the sample population that was submitted to this more detailed analysis included animals more or less evenly distributed over the collection period (and including the first and last hinds collected), and from each of the three collection areas.

The detailed determinations were made on the tissues of the various groups of the body into which it had been divided

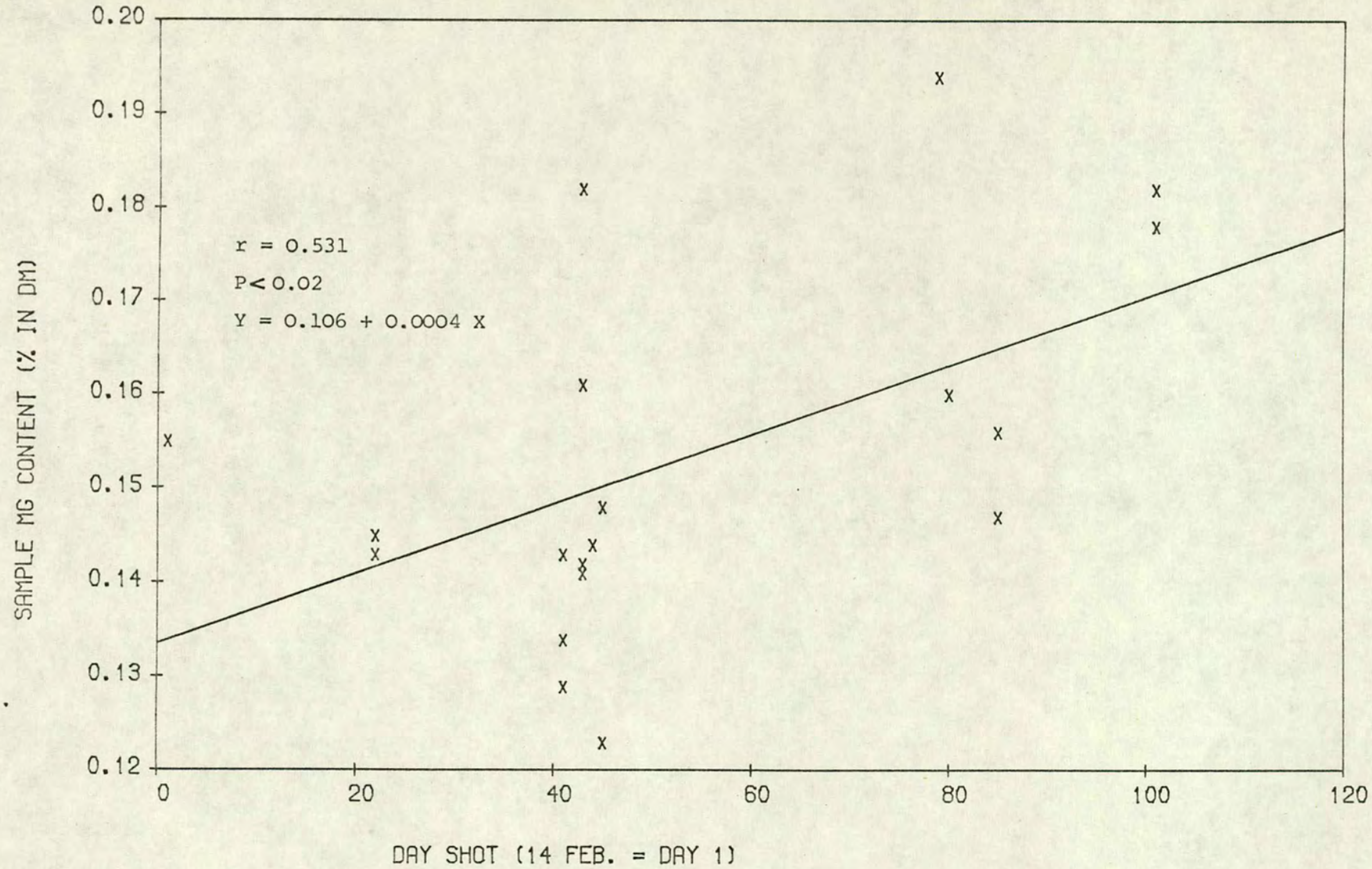


FIG. 3.4. INCREASE IN % MG IN SAMPLE DM

and minced. These were (see chapter 2 for a detailed description of the dissection of these joints):

Group 1: the butcher's retail cut of the shank of the haunch;

Group 2: the retail cut of the shank of the foreleg;

Group 3: the shoulder group, containing the shoulder prime cut, the brisket and the neck;

Group 4: the haunch prime cut, the flank, and the ribs and loin cuts;

Group 5: the remainder of the body (head, pelt, feet and internal organs), excepting the cannon bones and perirenal fat.

The DM, ash, nitrogen and fat contents of the muscle and bone tissues of Groups 1, 2 and 4, and of the associated fatty tissue of Group 4 (except for hind no. 24) were determined. Only the DM and fat contents of the associated fatty tissues of Groups 1 and 2 (and, for hinds nos. 32 and 35, of Group 3) were determined. Determinations were not made on the bone tissue of Group 3. Sub-cutaneous fatty tissue sufficient to be made up for chemical determination was only present in Group 4 of hind no. 17. Similarly, sufficient perirenal fat was present only in hinds nos. 17, 32 and 35, and then (excepting no. 17) only enough for DM and fat content to be determined. Group 5 (the offal portion of the body) was minced as a single sample, and therefore determinations could not be made on different tissues within it.

3.2.A. Changes in the composition of Group 1 (see Table 3.3)

3.2A.1. MUSCLE TISSUE COMPOSITION.

The DM and ash contents of the muscle tissue of the haunch shank were negatively but non-significantly correlated with time. The percentage of nitrogen in the muscle tissue appeared to increase as time progressed over the winter

Table 3.3: Major chemical components of the muscle, bone and fat tissues of Group 1, the haunch shank.

MUSCLE DM (%)	MUSCLE ASH (%) IN DM	MUSCLE NITROGEN (%) DM	MUSCLE FAT (% IN DM)
29.8400	4.3200	12.9400	7.1700
25.2500	5.3200	12.8900	5.8400
26.7200	4.5000	12.6300	2.5700
28.2400	4.0100	14.1200	1.5800
27.0800	3.9400	13.3000	3.8800
27.3400	4.1500	14.0800	0.8500

GO :

BONE DM (%)	BONE ASH (% in D.M.)	BONE NITROGEN (DM %)	BONE FAT (DM %)
89.5900	47.6900	3.9400	11.9500
79.5300	48.8700	4.3300	17.6600
85.7100	46.5300	4.5700	15.4300
71.8200	51.1700	5.2000	3.9500
79.2500	48.0000	4.9000	12.7600
64.0700	56.1700	5.2500	1.8500

GO :

FAT DRY MATTER (%)	FATTY TISSUE FAT(% in D.M.)
57.5300	47.6200
69.1500	80.2900
59.9100	23.1500
72.8900	27.6400
69.5500	44.9900
61.2200	14.2700

GO :

($r = 0.76$, $P < 0.1$). The fat content of the muscle tissue significantly decreased, from about 7% to 0.8% ($r = -0.83$, $P < 0.05$).

3.2A.2. BONE TISSUE COMPOSITION.

The DM content of the haunch shank bone tissue (the tibia and the fibula) decreased over the collection period from around 89.5% to around 64% ($r = -0.88$, $P < 0.05$), while the percentage of ash in the DM appeared to increase ($r = 0.68$, $P < 0.2$). The nitrogen content in the DM of the bone tissue was found to increase from around 3.9% to 5.2% ($r = 0.96$, $P < 0.005$). Interestingly, the fat content of the tibia and fibula of hind no. 17 was determined to be considerably lower than that of the next two hinds collected (11.9% as compared to an average of 16.5%; see Table 3.3). This variability results in a non-significant correlation between time and the fat content of these bones ($r = -0.62$, $P > 0.1$).

3.2A.3. ASSOCIATED FAT TISSUE COMPOSITION.

Only DM and fat content were determined for the fatty tissue associated with the haunch shank. Percent DM increased, while the fat content decreased (Table 3.3) over the collection period, but neither of these trends was statistically significant.

3.2B. Changes in the composition of Group 2 (see Table 3.4).

3.2B.1. MUSCLE TISSUE COMPOSITION.

The DM and ash contents of the muscle tissue of the shoulder shank were similar to those of the haunch shank muscle, and also showed no significant change over the collection period. The nitrogen content of the shoulder shank muscle was also similar to the nitrogen content of the haunch

Table 3.4: The major components of the muscle, fat and bone tissues of Group 2, the fore shank.

MUSCLE DM (%)	MUSCLE ASH (%) IN DM	MUSCLE NITROGEN (DM%)	MUSCLE FAT (% IN DM)
29.5000	3.6900	13.1600	7.5200
25.8900	4.0310	13.5000	4.2000
26.4300	5.0900	13.1600	4.1700
29.4300	4.1800	14.2800	0.5700
29.7600	4.0600	13.3500	4.5200
27.7000	4.7400	13.8000	0.3500

BONE DM (%)	BONE ASH (% in D.M.)	BONE NITROGEN (% in D.M.)	BONE FAT (DM %)
85.4400	52.2800	4.5900	14.3700
78.4400	44.4700	4.2500	14.8900
82.9000	45.8400	4.6900	14.1400
76.9500	62.9900	4.8200	3.1400
72.9900	52.4300	5.0400	14.2400
74.0100	60.5300	5.0600	2.1400

FAT DRY MATTER (%)	FATTY TISSUE FAT(% in D.M.)
70.6600	76.2000
46.9400	57.6200
43.6400	42.1000
46.2500	47.3400
51.3300	52.8600
53.5600	3.3200

shank muscle. As in that tissue, nitrogen in the shoulder shank muscle demonstrated a trend to increase in its percentage of the DM with the passage of time. The correlation was less ($r = 0.62$, $P < 0.1$) than that of haunch shank muscle nitrogen with time. The percentage of fat in the DM of the shoulder shank muscle was similar to that of fat in the haunch shank (around 7% at the beginning of the collection period), and also decreased significantly over the 100 days ($r = -0.84$, $P < 0.05$).

3.2B.2. BONE TISSUE COMPOSITION.

The DM content of the shoulder shank bone tissue (the radius and the ulna) was similar to that of the tibia and fibula at around 85% to 90% in the first hind, and dropped significantly over the collection period ($r = -0.92$, $P < 0.01$). The percentage of ash in the DM of the radius and ulna appeared to increase slightly with time, but the correlation was not significant ($r = 0.59$, $P < 0.1$). The fat content of the radius and ulna was similar to that of the tibia and fibula, and also appeared to decrease with time ($r = -0.68$, $P < 0.2$).

3.2B.3. ASSOCIATED FATTY TISSUE COMPOSITION.

As with the Group 1 tissue, only DM and fat content were determined for the associated fat of the shoulder shank joint. As in the haunch shank fatty tissue, that in the shoulder shank showed no significant change in the amount of DM it contained. Unlike that in the haunch shank, however, the shoulshank fatty tissue showed a significant drop in fat content over the collection period; from over 76% to only about 3% ($r = -0.78$, $P < 0.1$).

3.2C. Changes in the composition of Group 3 (see Table 3.5).

3.2C.1. MUSCLE TISSUE COMPOSITION.

Unlike the muscle tissue of the shoulder and haunch shanks, the DM content of that in the upper shoulder, brisket and neck was found to decrease. The drop was slight, but significant ($r = -0.85$, $P < 0.05$), from around 30% to 26%. Also unlike the muscle tissues of these other joints, ash content appeared to increase over the collection period ($r = 0.76$, $P < 0.1$). Nitrogen content was similar to that in the muscle of the shanks, however (around 11% to 13% in the first hind collected), and similarly increased in the DM over time ($r = 0.95$, $P < 0.005$). Fat content in the DM of the upper shoulder and neck muscle tissue was higher than it was in the muscle in the shanks of the first hind collected (16% as compared to around 11%), but significantly decreased ($r = -0.89$, $P < 0.005$) to a level similar to those in the shank muscles (less than 1%) in the last hind collected.

3.2C.2. ASSOCIATED FATTY TISSUE COMPOSITION.

The DM content of the associated fatty tissue of the upper shoulder and neck was similar to that of this tissue from the shanks of hind no. 17. However, it decreased in the fatty tissue of the hinds collected later ($r = -0.91$), $P < 0.01$), which was unlike the DM contents of the fatty tissue of their haunch shanks. The ash content of the fatty tissue of the upper shoulder and neck increased significantly ($r = 0.98$, $P < 0.025$) in the four hinds for which determinations of it were made. The nitrogen content of the associated fatty tissue of these four hinds also increased significantly ($r = 0.99$, $P < 0.005$). The fat content of the DM of the fat tissue of the upper shoulder and neck decreased dramatically in all six

Table 3.5: Levels of composition of the major components of the tissues of Group 3, the shoulder and neck

MUSCLE DM (%)	MUSCLE ASH (% IN DM)	MUSCLE NITROGEN (DM %)	MUSCLE FAT (% IN DM)
29.7200	3.4800	11.3600	16.1400
28.8800	3.8600	12.7300	8.6400
30.1400	4.1500	12.1300	5.5600
27.8800	4.8500	12.9900	6.3900
26.0200	3.8000	13.0900	6.4100
26.5500	4.6200	13.8000	0.1130

16 GO :

FAT DRY MATTER (%)	FAT ASH (% IN DM)	FATTY TISSUE NITROGEN (% in D.M.)	FATTY TISSUE FAT(% in D.M.)
69.0800	0.7800	1.9400	82.7600
51.3600	1.5600	3.9600	66.2600
54.4400	1.7500	4.4400	62.1200
37.9200	3.1000	6.9300	22.2200
41.6800	0.0000	0.0000	40.1850
45.1300	0.0000	0.0000	40.1800

17 GO :

hinds from over 80% to around 3% ($r = -0.93$, $P < 0.005$). This decrease is similar to that occurring in the fat content of the DM of the fat tissue of the shoulder shank.

3.2D. Changes in the composition of Group 4 (see Table 3.6).

3.2D.1. MUSCLE TISSUE COMPOSITION.

The DM content of the muscle in the upper haunch, loin and ribs, like that of muscle in the shanks but unlike that of muscle in the shoulder and neck, did not appear to change over the period examined. Ash content in the DM also showed no significant change. Nitrogen content of the DM was similar to that of the other muscle tissues of the body, and was found to increase significantly with time ($r = 0.76$, $P < 0.05$). The fat content of the muscle of this Group (around 12%) in the first hind to be collected was more similar to that of the muscle tissue of the shoulder and neck (around 16%) than was that of the muscle in the shanks (around 7%). However, it showed a significant decrease ($r = -0.85$, $P < 0.05$), and in the last hind was at a level of less than 1%, similar to the levels of fat in the muscle tissues of the rest of the body.

3.2D.2. BONE TISSUE COMPOSITION.

The DM content of the bone tissue of the upper haunch, loin and ribs group was found to be considerably lower than the DM content of the bones of the shanks, by around 20%. Perhaps for that reason, DM in the bone tissue of Group 4 decreased more slowly than did DM in bone tissue elsewhere (cf. regression coefficients in Tables 3.3-6), and also was less negatively correlated with time ($r = -0.66$, $P < 0.1$). Like that in bone elsewhere in the body, the percentage ash in the DM of the bone tissue of Group 4 appeared to increase

MUSCLE DM (%)	MUSCLE ASH (%) IN DM	MUSCLE NITROGEN (%) DM	MUSCLE FAT (% IN DM)
28.9400	3.9000	11.8600	12.4200
25.6600	6.8400	13.3600	3.4700
28.1100	3.6300	12.2400	7.7900
30.2600	4.9400	13.6300	2.1300
28.3200	4.3000	13.0000	5.7000
26.7300	6.2400	13.3300	0.5900

22 GO :

BONE DM (%)	BONE ASH (% IN D.M.)	BONE NITROGEN (% DM)	BONE FAT (DM %)
65.7500	31.1100	4.9100	21.4900
58.0600	34.3600	5.6400	20.7000
64.0700	38.2700	5.4600	17.6000
57.9000	41.8600	5.9500	10.0300
60.6000	34.9800	5.2300	15.7100
59.9300	43.1800	5.8500	1.7900

23 GO :

FAT DRY MATTER (%)	FAT ASH (% IN D.M.)	FATTY TISSUE NITROGEN (% IN D.M.)	FATTY TISSUE FAT (% IN D.M.)
71.8200	0.7200	2.5000	81.3200
43.9600	2.3000	8.7900	41.5500
0.0000	0.0000	0.0000	42.1200
47.1000	2.2700	7.2500	49.1900
38.4200	4.1900	12.2200	13.4700

24 GO :

SUB-CUT. FAT DM (%)	SUB-CUT. ASH (% IN D.M.)	SUB-CUT. NITROGEN (% IN D.M.)	SUB-CUT. FAT (% IN D.M.)
78.1200	0.7400	269.0000	79.9300
0.0000	0.0000	0.0000	0.0000
0.0000	0.0000	0.0000	0.0000
0.0000	0.0000	0.0000	0.0000
0.0000	0.0000	0.0000	0.0000
0.0000	0.0000	0.0000	0.0000

25 GO :

Table 3.6: Levels of the major chemical components of the muscle, bone and fatty tissues of Group 4, the prime cut of the haunch, and the ribs and loin.

over the collection period ($r = 0.78$, $P < 0.1$). The nitrogen content of the DM also appeared to increase ($r = 0.68$, $P < 0.2$). The fat content of the bone tissue in this Group in hind No. 17 was somewhat higher (around 21%) than it was in the DM of the bone tissues elsewhere in her body, but had dropped to a level in the last hind similar to those in the other Groups of her body (around 2%). The fat content in DM here was more closely negatively correlated with time ($r = -0.84$, $P < 0.05$) than it was in bone tissue elsewhere.

3.2D.3. SUB-CUTANEOUS FATTY TISSUE.

Hind no. 17 was the only one, of the six on which detailed determinations were made, to have sufficient subcutaneous fat (which was located in the haunch, loin and ribs) for a sample to be prepared for analysis. The percent DM and the percentages of ash, nitrogen and fat in it, were similar in this tissue to the percentages of them in the associated fatty tissues located elsewhere in hind no. 17 (Table 3.3-7).

3.2D.4. ASSOCIATED FATTY TISSUE COMPOSITION.

The DM content of the associated fatty tissue of this group of the body (around 72%) was similar to that of fat elsewhere in hind no. 17, but in the last hind collected (no.35) it was lower here than DM in fat in the rest of her body. Like the DM content of the fatty tissue of the shoulder shank and upper shoulder and neck, but unlike that in the haunch shank, the DM content of the fatty tissue here in Group 4 significantly decreased over the collection period ($r = -0.87$, $P < 0.05$). The percentage ash in the DM increased over time ($r = 0.89$, $P < 0.05$), and so too did the percentage of nitrogen ($r = 0.85$, $P < 0.05$). The fat content of the DM

of Group 4 fatty tissue decreased less than it did in fat tissue elsewhere, except in the haunch shank, but the drop was nonetheless significant ($r = -0.87$, $P < 0.05$).

3.2E. Changes in the composition of Group 5 (see Table 3.7).

3.2E.1. COMPOSITION OF THE HEAD, PELT & INTERNAL ORGANS.

The DM content of the body (sampled as a whole) other than the butcher's carcass was found to decrease significantly ($r = -0.90$, $P < 0.02$) from around 39% to 29% over the collection period. The percent ash in the DM did not change, but the percent nitrogen in the DM increased ($r = 0.89$, $P < 0.05$). The fat content of the DM of the offal component of the body (not including perirenal fat) was found to be negatively but non-significantly correlated with time ($r = -0.56$, $P \leq 0.2$). However, it can be seen from Table 3.7 that hind no. 20 had an apparently unusually low fat content in this part of her body; if her value be removed, the correlation becomes highly significant, even in spite of the loss of a degree of freedom ($r = -0.91$, $P < 0.02$). This point will be discussed in Chapter 5.

3.2E.2. CANNON BONE COMPOSITION (Table 3.7).

The percent DM in the cannon bones was lower in the animals from Glen Feshie than it was in the bones of the hinds from elsewhere, and it was as high in the last hinds to be collected as it was in the first one; with so small a sample no explanation for these anomalies can be offered. The percentage of ash in the DM showed a distribution between animals similar to that in DM percentage. However, nitrogen content in the DM was found to show a more or less steady drop over the collection period ($r = -0.81$, $P < 0.05$). The fat content

OFFAL DM (%)	OFFAL ASH (% D.M.)	OFFAL NITROGEN (% D.M.)	OFFAL FAT CONTENT(% D.M.)
38.3200	8.3100	28.3100	7.7500
36.5600	12.8800	3.6900	9.6500
39.1600	14.8000	16.4800	8.6400
31.2500	13.4300	13.3600	9.6100
31.4700	10.9500	17.3100	9.3100
29.4100	12.2900	7.3800	10.1800

25 GO :

CANNON BONE DM	CANNON ASH (% D.M.)	CANNON NITROGEN (% D.M.)	CANNON FAT (% D.M.)
84.0400	50.0800	6.0000	19.6400
72.2600	44.9100	5.4000	14.2600
72.7600	42.6400	5.5600	14.7000
80.6800	51.1600	5.4500	5.5200
83.4100	50.7100	5.2500	7.6800
82.7700	55.6200	5.4300	2.1000

26 GO

KIDNEY FAT DM %	KIDNEY FAT CONTENT(%)
85.1000	91.4700
0.0000	0.0000
0.0000	0.0000
0.0000	0.0000
41.0000	57.8900
26.2100	20.7800

27 GO :

Table 3.7: The levels of the major chemical components in the tissues of Group 5, the offal, or non-carcass, component of the body.

in the DM of the cannon bones of the first hind collected was similar to that in her bone tissue from Group 4, and higher than that in the bone tissue of Groups 1 and 2, but in the last hind, fat in the cannon bones had dropped to a level similar to that found in her bone tissue elsewhere (about 2%). It is interesting to note that the fat content in the DM of the cannon bones was almost perfectly negatively correlated with time ($r = -0.98$, $P < 0.005$). This finding lends support to the use of visual assessment of cannon bone marrow as an indicator of the condition of animals.

3.2E.3. PERIRENAL FAT COMPOSITION (Table 3.7).

Sufficient perirenal fat to allow a sample to be prepared was present only in three (nos. 17, 32 and 35) of the six hinds on which these more detailed determinations were made. In spite of this, the DM content of the perirenal fat tissue was found to be very closely negatively correlated with time ($r = -0.99$, $P < 0.05$), and dropped from around 85% in the first hind collected to 26% in the last. With only one degree of freedom, the apparently high negative correlation between fat content in the DM of the perirenal fatty tissue and time was not significant ($r = -0.92$, $P < 0.2$). The fat content of the DM of the perirenal fat of the last hinds collected was considerably lower than that in the first hind (only 20% as compared to 91%); this is discussed further in Chapter 5.

3.3. A summary of the changes occurring in the chemical composition of the tissues of the half carcass over the late winter and spring.

3.3.1. CHANGES IN THE COMPOSITION OF MUSCLE TISSUE.

Changes in the DM content of muscle tissue varied within different parts of the carcasses of the six hinds analysed in

detail. The DM content of Group 2 (the shoulder shank) muscle was very slightly (and non-significantly) positively correlated with the passage of time, while that of the Group 1 (haunch shank) and Group 4 (upper haunch, loin and ribs) muscle was negatively but non-significantly correlated with time. The DM in the muscle of Group 3 (the upper shoulder, brisket and neck) significantly dropped over the period from which the hinds were taken.

The percentage of ash in the DM of the muscular tissue of Group 1 was found to be very slightly (and non-significantly) negatively correlated with time. Percent ash increased in the muscle tissue of the other groups, although only the increase in Group 3 was found to be statistically significant. The percentage of nitrogen increased in the muscle tissue of all four groups. The increase in the Group 2 muscle was not significant, but those of the other three groups were, and it seems likely that if a larger sample had been available, the increase in Group 2 would have been found to be significant as well.

The fat content of all muscular tissue was found to decrease significantly over the period investigated. In the first hind collected (hind 17) about 8% of the DM of the muscle of Groups 1 and 2 was fat, and about 15% of that in Groups 3 and 4 (the weight of fat in the various tissues is given and discussed in Chapter 5). None of the muscle tissue of the last hind collected (hind 35) contained more than 1% of fat in the DM.

3.3.2. CHANGES IN THE COMPOSITION OF BONE TISSUE.

The DM content of bone decreased in all of the three groups for which it was determined. The percentage DM in the

bone of Groups 1 and 2 was significantly negatively correlated with the passage of time, and had a larger sample been available, the decrease in Group 4 probably would have been found to be so as well.

The ash content of the bone tissue of all three groups was positively correlated with the passage of time. Only the correlation for that of Group 4 was significant, but I think that there is a genuine trend for per cent ash to increase in the other bone tissue as well.

The per cent nitrogen in the DM of the bone tissue of all three groups also increased. The correlation of Group 4 nitrogen with time was not significant, but again it seems likely that it would have been so from a larger sample.

The fat content of the bone of all three groups decreased, although only the Group 4 decrease was statistically significant. However, I think that fat is genuinely disappearing from bone tissue over the period examined.

3.3.3. CHANGES IN THE COMPOSITION OF ASSOCIATED FATTY TISSUE.

The DM content of the fatty tissue of Group 1 was positively (but non-significantly) correlated with time, but DM content of the fatty tissue from the other areas of the carcass dropped. It seems likely that the DM content of fatty tissue generally drops over the winter period, just as it does in muscle and bone.

Ash and nitrogen percentages were determined only in the fatty tissues from Groups 3 and 4. The percentages of both significantly increased in both these groups.

The fat content of the fatty tissue from all four groups decreased over the period examined. The drops were statistically significant for Groups 2, 3 and 4. The decrease in

the tissue from Group 1 was not significant because of the relatively high level of fat in this tissue in hind 32. It can be seen from the figures in Tables 3.3 to 3.7 that this particular beast had relatively high levels of fat in all the tissues of her carcass. This point is discussed in Chapter 5, but I will suggest here that this hind, by the 9th of May (when she was collected), had already begun to improve in condition.

3.4. The energy status of wild Scottish red deer hinds during late winter and spring.

The hypothesis proposed at the beginning of this chapter appears to be amply justified by the results of the analyses reported. In spite of the variations in age, weight, and, presumably, skeletal size in the hind sample population, their empty body gross energy contents showed a very highly significant correlation with the passage of time over the collection period ($r = -0.84$, $P < 0.001$). Gross energy content fell from a maximum value of around 130 megacalories (Mcal) in the first hind collected (no. 17) to an averaged minimum of only about 70 Mcal in the two collected last at the end of May (nos. 34 and 35). This drop was not the result of younger or skeletally smaller animals being sampled at the end of the period; the loss per kg of empty body weight was even more highly correlated with date ($r = -0.88$, $P < 0.001$; see Figure 3.5). Also, there was no significant correlation between date and the age of the sampled hinds (see Table 2.1). Rate of gross energy loss is estimated to have been around 8 kcal per kg empty body weight per day; over the 100 days the energy content of the hinds collected dropped by around 55 percent (Table 3.8, Figure 3.5).

Table 3.8: The estimated amounts of gross energy, and weights of dry matter, nitrogen, protein and fat in the empty bodies of the collected hinds.

EMPTY-BODY ENERGY (MCAL)	WEIGHT OF E-B DM (KG)	WEIGHT OF E-B NITROGEN (KG)	EMPTY-BODY PROTEIN WT (KG)	EMPTY-BODY FAT WEIGHT (KG)
130.3322	22.3808	1.8068	11.2925	6.4188
99.2490	17.2490	1.6507	10.3170	3.9259
118.6100	20.8593	1.8287	11.4296	5.1314
82.2447	15.0579	1.5108	9.4422	2.9694
108.9297	19.1643	1.7777	11.1105	4.5458
101.0554	17.9450	1.5596	9.7475	4.2063
76.7221	15.7108	1.7288	10.8051	2.0487
105.1774	19.4040	1.8570	11.6060	4.1757
106.8437	18.8600	1.7242	10.7761	4.2850
95.9180	17.0688	1.6697	10.4354	3.4615
106.4187	19.3545	1.8544	11.5897	3.8090
111.6123	20.5249	1.8314	11.4465	3.9736
112.5089	19.5978	1.7458	10.9111	4.2410
91.9909	18.3505	1.7679	11.0493	2.2828
79.5368	15.1392	1.6323	10.2019	2.4223
71.3658	13.2932	1.3781	8.6131	1.5367
77.4292	15.4840	1.6054	10.0336	1.1458
65.1798	13.4386	1.3358	8.3487	0.9568
69.0046	14.1036	1.4884	9.3022	0.8293

20 GO :

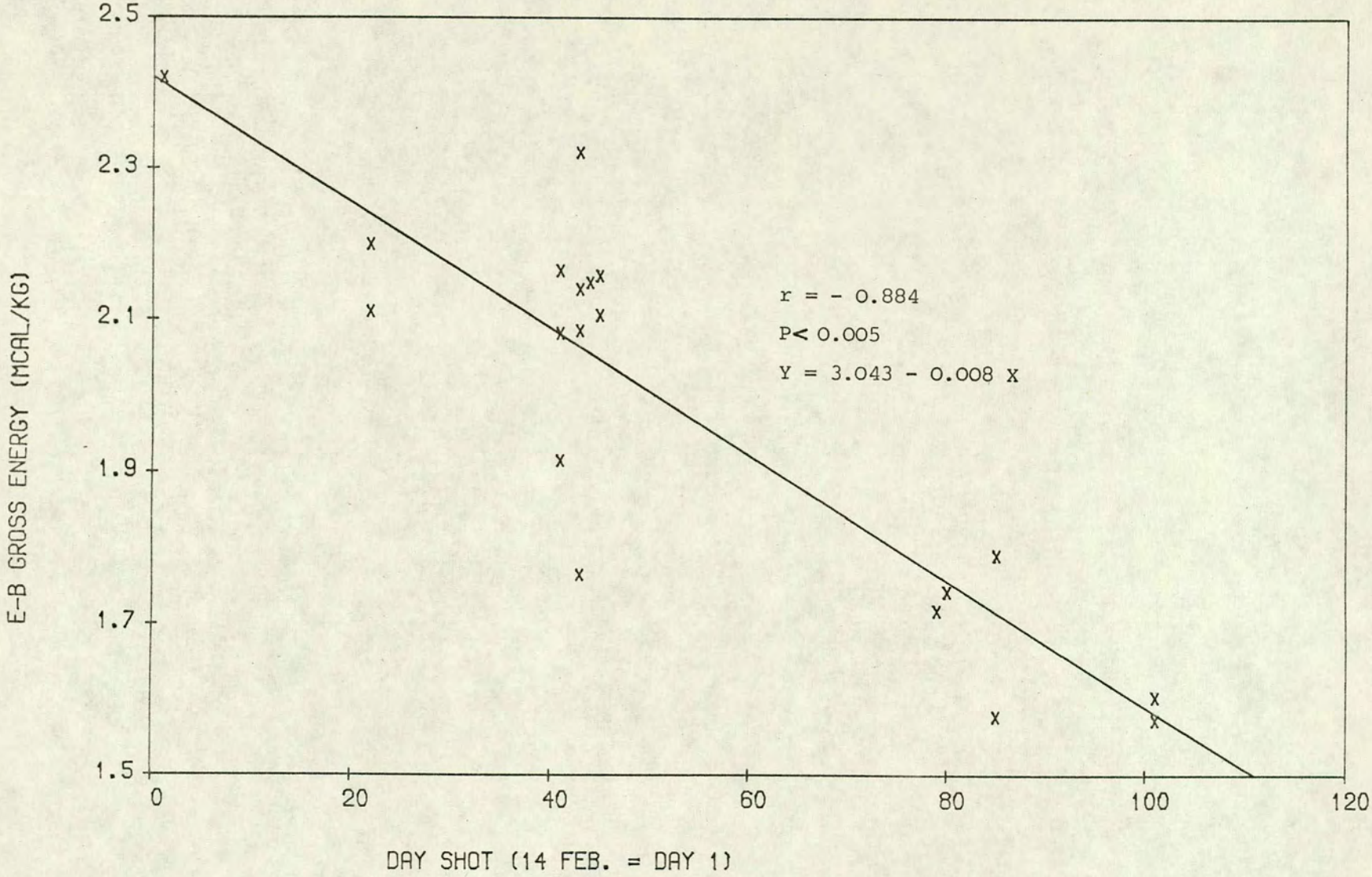


FIG. 3.5. EMPTY BODY ENERGY LOSS

That the weight losses so characteristic of wild Scottish hinds during the winter are the result of their being in this state of negative energy balance is supported both by the results reported in this chapter and the data from the physical dissections made on the sampled hinds' bodies (see Chapter 4). The variation in empty body weight (Table 2.1) is closely and highly significantly correlated with its gross energy content ($r = 0.82$, $P < 0.001$). This correlation is largely due to the influence of energy status on the amounts of fat present in the body. The primary function of body fat is to act as a readily-available reserve supply of energy. Although energy also can be provided by the katabolism of muscle protein, when dietary energy intake is insufficient to meet metabolic requirements the deficit is usually made up by the katabolism of fatty tissue. As expected, the variation in gross energy content of the empty bodies of the hinds examined in this study, as represented by the samples analysed, was very highly correlated with variation in the amount of chemically determined fat in the bodies ($r = 0.93$, $P < 0.001$). The drop in gross energy content over the collection period was accompanied by a drop in fat content of the samples (which decrease was itself closely negatively correlated with time: $r = -0.92$, $P < 0.001$).

Variation in the larder weights of the sampled hinds is more closely correlated with both gross energy content ($r = 0.84$, $P < 0.005$) and weight of chemically determined fat ($r = 0.72$, $P < 0.005$) than is that in empty body weight; in Chapter 4 it is proposed that larder weights are better measurements to use when comparing 'condition' (i.e. the amounts of fat, and hence energy reserves, animals contain) between ruminants than are either live or empty body weights. The variation in larder

weights by the hind sample is not perfectly correlated with fat content for a variety of reasons. Since it was impossible to collect a sample of similarly aged animals, the animals collected vary in weight due to differences in age (the correlation between age and larder weight in the sample was found to be: $r = 0.51$, $P < 0.05$). In spite of this, variation in larder weight is more highly correlated with fat content than with age, and it seems likely that if it had been possible to procure hinds of the same age for sampling, the correlation between larder weight and fat content would have been even higher (some variation can always be expected to arise due to the individuality of animals).

If it be accepted that the 19 hinds collected for this study are representative of the majority of wild Scottish hinds, the regression equation derived from them can be accepted as estimating that an average adult hind contains around 6 kg of body fat in mid-February. By the end of May this has dropped to only about 860 g, which represents an average loss of about 50 g per day. This loss is greater than would be apparent by dissecting and weighing fatty tissue. The actual chemical fat content of the fatty tissue in late May has been seen to be only 3% to 20% of the DM of the tissue, which has itself been decreasing (see sections 3.2A to 3.2E). By the end of May, therefore, a sample of fatty tissue weighing 100 g may in fact only contain 4 g of fat. The majority of the weight of the tissue would be contributed by water, while the increase in the percentage of nitrogen in the fatty tissue of the upper shoulder and neck, and upper haunch, loin and ribs groups show that the relative proportions of connective tissue, and possibly of

blood, have increased in relation to fat.

As has been mentioned earlier (see section 3.1.4), the increase in the percentage of nitrogen in the DM of the samples representative of the empty bodies is probably simply the result of the steady disappearance of fat from the DM. The weight of protein in the empty body (calculated from the percentage of nitrogen in the representative samples, on the assumption that weight of protein is approximated by the weight of nitrogen multiplied by 6.25; MacDonald et al., 1973; see Table 3.8), is significantly negatively correlated with time ($r = -0.65$, $P < 0.005$). Whether or not this is an indication that muscle tissue is also being katabolised to meet energy requirements as fat disappears from the body is discussed in Chapter 5.

The results of the detailed analyses of the levels of DM, ash, nitrogen and fat in the various tissues and regions of the body, and those of the analyses of changes in mineral content in the body, are discussed in Chapter 5. Along with the data presented in the next chapter, on the physical changes found in the bodies of the sample hinds, these results are used to propose a descriptive model of the physiology of severe undernutrition, as suffered by many wild Scottish red deer hinds over the late winter/spring period. From the results presented in this chapter, if it be accepted that the sample of 19 hinds collected for this study are representative of the majority of adult wild Scottish yeld hinds, it would appear that the majority of wild Scottish hinds are annually subjected to a prolonged and continuous period of negative energy balance during the winter and spring months, and that this is a result of severe under-

nutrition coupled with the energy demands made on them by pregnancy and their environment.

CHAPTER 4. Physical Changes in the Bodies of the Collected Hinds.

In addition to the changes in chemical composition reported in the last Chapter, the possibility that physical changes are occurring in the bodies of wild, pregnant Scottish red deer over the period mid-February to the end of May also was investigated. The weights of the different body parts (e.g. head, pelt, internal organs), and of the dissected muscle, bone and fatty tissues of the 19 sampled hinds had been recorded during dissection. These weights have been submitted to correlation and regression analysis in relation to the passage of time (in the same way that chemical changes were analysed in the last chapter), to establish which of them are statistically significant trends over the period of collection. The results of these analyses are reported in this Chapter.

4.1. Body weights changes.

The live-weights of the sample hinds were calculated by summing the larder weights (i.e., the weights taken on arrival at the estate larders or the Carcass Evaluation Unit, which excluded the weight of the blood lost during exsanguination at the time of killing, and the weights of the digestive tract and conceptus, which had been removed in the field), with the weights of digestive tract and conceptuses recorded when removed from the body. Some blood loss was unavoidable, and the live-weights given in Table 2.1 take no account of the weights of this loss. The amount of blood remaining in the body and thus being included in the weight taken on arrival at the larder presumably varied somewhat between animals (for the reasons given in

Chapter 2). However, the weight of blood lost has been assumed to be small enough to allow it to be ignored.

The estimated live-weights of the hinds were found to be slightly, but non-significantly negatively correlated with the passage of time ($r = -0.18$, $P > 0.1$; see Table 4.1). The non-significance of this correlation is not surprising, considering the differences in age, body size and weight of the conceptus and of the contents of the digestive tract, that there must have been between the sampled hinds. It is interesting that in spite of differences in age, and presumably in skeletal size and contents of the digestive tracts, when the weight of the conceptus is subtracted, the variation in body weight becomes significantly negatively correlated with the passage of time ($r = -0.49$, $P < 0.05$). On removal of the variance caused by differences in weight of the contents of the digestive tract (rumen fill and faeces), the resulting 'empty body' weight (i.e. conceptus- and ingesta-free) was found to be slightly more closely negatively correlated with time ($r = -0.51$, $P < 0.05$).

It is interesting that the larder weights of the sampled hinds (i.e. empty body weights less the weights of the digestive tract) were even more closely negatively correlated with the passage of time than were empty body weights (Figure 4.1). Mitchell et al. (1977) propose that larder weight is a better measurement for comparative purposes of the condition of individual ruminants, because the alimentary tract is so large (accounting for 20 to 40% of live-weight; in this study rumen fill alone was found to vary from 9.0 to 16.3 kg). Whether the better correlation found between time and larder weight, rather than empty body weight,

Table 4.1. Correlation matrix between the date a hind was shot and various types of body weight measurements (see text for explanation of weights)

	TIME (14 FEB=DAY 1)	LIVE WEIGHT (KG)	CONCEPTUS-FREE LIVE WEIGHT	EMPTY-BODY WEIGHT (KG)
LIVE WEIGHT (KG)	-0.189 50.000% 3.6%			
CONCEPTUS-FREE LIVE WEIGHT	-0.491 4.000% 24.1%	+++++ 0.943 0.001% 88.9%		
EMPTY-BODY WEIGHT (KG)	-0.512 3.000% 26.2%	+++++ 0.924 0.001% 85.3%	+++++ 0.983 0.001% 96.7%	
LARDER WEIGHT (KG)	-0.575 1.000% 33.0%	+++++ 0.886 0.001% 78.5%	+++++ 0.973 0.001% 94.7%	+++++ 0.989 0.001% 97.8%

16 GO :

N.B.: -

The first value is r;

the second value is P;

the third value is R^2.

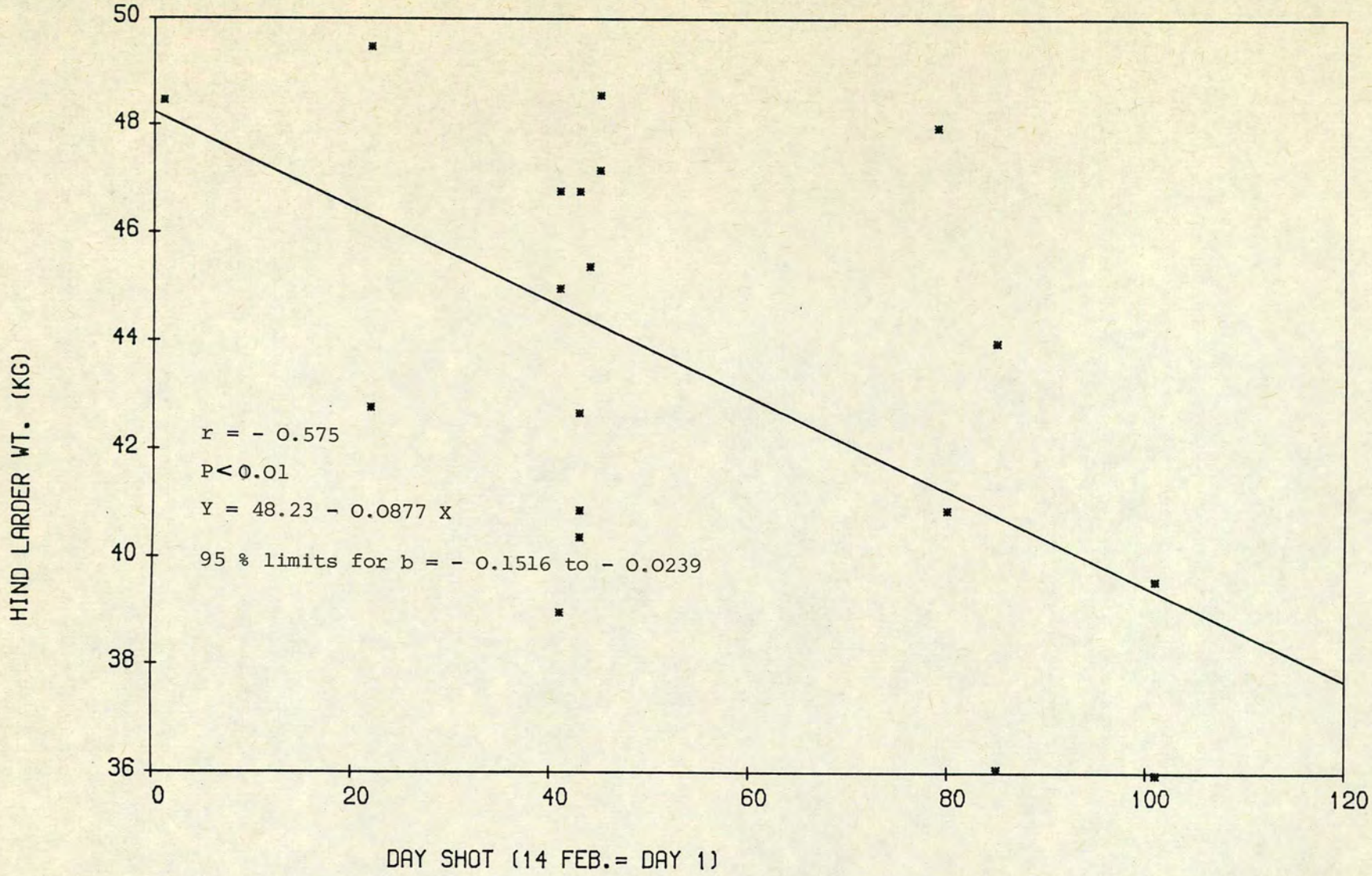


FIG. 4.1: DROP IN LARDER WEIGHT OVER TIME

was due simply to differences in age and individual variation in body size, or whether other factors were also involved, is discussed in Section 4.2 below.

It should be noted that an error may have arisen during the taking of larder weights, through variation in the amounts of moisture held in the pelt when the animals were weighed. This may have varied depending on whether or not it were raining when a hind was shot; animals also on occasion unavoidably were dragged through water-courses while being brought back to the Land-rover or pony by which they were transported off the hill. It was not practical to attempt to measure the size of such error: the body cavities of the hinds were open, and any attempt at weighing the pelt before and after drying would simply have introduced a new error, by increasing evaporative losses from the tissues (removal of the pelt immediately after arrival at the larder was never practicable, for one reason or another). Purely as a guess, I suppose that an animal which is shot on a day of very heavy rain, or which had been dragged through a burn (stream) may weigh up to 3 kg more than when its pelt is dry.

In spite of the criticisms which have been levelled against the using of body weights to compare various parameters, and particularly condition, between individuals or populations, more accurate analytical techniques often are not available, and body weights remain one of the most readily available bases for such comparisons. To test the possibility that the decrease in all the weight measurements of the bodies, less conceptuses, of the hinds collected in the present study was due to younger, smaller animals having been collected during the latter part of the collection period, I analysed

the relationship between age and body weights. As expected, body weights and age were found to be significantly correlated (Table 4.2). The negative correlation between age and date shot indicates that slightly younger animals were shot as the collection period progressed. However, the correlation is not significant, and further testing found no significant difference between the average age of the first half ofthe sample, and that of the second half.

Table 4.2. Correlations between age and body weight measurements, and date shot.

	Live weight less conceptus	Empty body weight	Larder weight	Date shot
Age	$r = 0.58, P<0.01$	$r = 0.51, P<0.05$	$r = 0.51, P<0.05$	$r = -0.19, P<0.5$

Since the first three and last four hinds were collected from the same estate (Corrour), the downward trend in weights observed is unlikely to be due to possible differences in genotype or growth rates between the populations of the collection areas; I propose that the trend is a genuine demonstration of the body weight losses which wild Scottish hinds characteristically undergo during the winter and spring months.

4.2. The location of weight losses within the body.

Having accepted the proposition that the sample hinds had been experiencing the losses in gross body weight typical of wild hinds, I examined the dissection data to see where within the body these losses were occurring. The problem again arose that since the sample population consisted of animals which were of differing ages, variation in gross weights of the parts of the body due to age may mask that due to an insufficient intake of dietary energy as time pro-

gressed. However, since all the hinds comprising the sample were within the 'prime' age group (4 to 10 years), it seemed possible that the proportions of empty body weight contributed by the organs and other parts of the body had reached relatively constant values. To test this, I analysed the percentages of empty body weight contributed by various parts of the body in relation to the age of the hinds (Table 4.3). No significant correlation was found between the age of a hind and the percentage of her empty body weight which was contributed by the full or empty gut, empty stomach, liver, lungs and trachea (weighed as a single unit), kidneys, diaphragm, heart or pelt. A negative correlation was found between age and per cent head weight ($r = -0.41$, $P<0.07$). This is not surprising since it is well known that the head and brain of mammals have high growth coefficients, indicating that they develop rapidly early in life.

The percentages of the empty body weight contributed by the head, pelt and internal organs, and by the butcher's half carcass and the muscle, bone and fatty tissues of which the half carcass is composed, were analysed with respect to the passage of time (Table 4.4).

The percentage empty body weight contributed by the weight of the head was found to increase significantly over the 100 day period ($r = 0.67$, $P < 0.01$). No significant correlation was found between time and the percent full gut weight. The percentage empty body weight contributed by the empty gut was found to increase significantly, however ($r = 0.55$, $P < 0.02$). The percentage empty body weight contributed by the empty stomach or by the liver did not appear to change. There was an indication that the percent contributed by the lungs and trachea (weighed as one unit)

	ESTD. HIND AGE (YEARS)	ESTD. HEAD % E-B WT.	ESTD. FULL GUT % E-B WT.	EMPTY GUT % E-B WT.	EMPTY STOMACH % E-B WT.
STD. HEAD % E-B WT.	+				
	-0.447				
	5.000%				
STD. FULLGUT % E-B WT.	.	.			
	-0.169	-0.214			
	50.000%	60.000%			
MPTY GUT % E-B WT.	.	.	++		
	-0.141	0.273	0.515		
	60.000%	30.000%	2.000%		
MPTY STOMACH % E-B WT.	.	.	.	--	
	0.064	0.015	-0.361	-0.521	
	80.000%	95.000%	10.000%	2.000%	
IVER % OF E-B T.	.	.	------	.	.
	0.139	0.259	-0.762	-0.382	0.371
	60.000%	30.000%	0.010%	10.000%	10.000%

7 GO :

	ESTD. HIND AGE (YEARS)	LUNGS&TRACHEA % E-B WT.	KIDNEYS % OF E-B WT.	DIAPHRAGM % OF E-B WT.	HEART % OF E-B WT.
UNGS&TRACHEA % E-B WT.	.				
	0.046				
	80.000%				
IDNEYS % OF E-B WT.	.	.			
	0.238	0.208			
	30.000%	60.000%			
IAPHRAGM % OF -B WT.	.	.	+		
	0.076	0.433	0.466		
	80.000%	6.000%	4.000%		
EART % OF E-B T.	.	.	.	.	
	-0.187	-0.337	0.214	0.245	
	60.000%	20.000%	60.000%	30.000%	
ELT % OF E-B W.	.	.	.	.	.
	-0.153	0.368	-0.250	0.134	0.196
	50.000%	10.000%	30.000%	60.000%	60.000%

8 GO :

Table 4.3. Correlation matrices between the age of the hinds (as estimated by the dental cement layers method) and the percentages of empty-body weight contributed by the various organs or parts.

ESTD. FULLGUT % E-B WT.	.				
	-0.334				
	20.000%				
	11.1%				
EMPTY GUT % E-B WT.	+++	++			
	0.552	0.515			
	1.000%	2.000%			
	30.5%	26.5%			
EMPTY STOMACH % E-B WT.	.	.	--		
	-0.151	-0.361	-0.521		
	50.000%	10.000%	2.000%		
	2.3%	13.0%	27.1%		
LIVER % OF E-BWT	.	------	.	.	
	0.316	-0.762	-0.382	0.371	
	20.000%	0.010%	10.000%	10.000%	
	10.0%	58.1%	14.6%	13.8%	

TIME (14 FEB=DAY 1)	ESTD. FULL GUT % E-B WT.	EMPTY GUT % E-B WT.	EMPTY STOMACH % E-B WT.

27 GO :

Table 4.4.(continued below). Correlation matrix between time and the percentage of empty-body weight contributed by various organs and parts of the body.

LUNGS&TRACHEA % E-B WT.	.				
	0.381				
	10.000%				
	14.5%				
KIDNEYS % OF E-B WT.	.	.			
	0.153	0.208			
	50.000%	60.000%			
	2.3%	4.3%			
HEART % OF E-B WT.	.	.	.		
	-0.012	-0.337	0.214		
	96.000%	20.000%	60.000%		
	0.0%	11.3%	4.6%		
DIAPHRAGM % OF E-B WT.	+	.	+	.	
	0.453	0.433	0.466	0.245	
	5.000%	6.000%	4.000%	30.000%	
	20.5%	18.7%	21.8%	6.0%	
PELT % OF E-B WT	.	.	.	.	.
	0.233	0.368	-0.250	0.196	0.134
	70.000%	10.000%	30.000%	60.000%	60.000%
	5.4%	13.6%	6.3%	3.9%	1.8%

TIME (14 FEB=DAY 1)	LUNGS&TRAC HEA % E-B WT.	KIDNEYS % OF E-B WT.	HEART % OF E-B WT.	DIAPHRAGM % OF E-B WT.

28 GO :

increased ($r = 0.38$, $P < 0.1$). The percentage contributed by the kidneys did not appear to change, but that contributed by the diaphragm was found to increase ($r = 0.45$, $P < 0.06$). The contribution by the heart, and that by the pelt, did not appear to change.

The percentage of the empty body weight contributed by the butcher's half carcass did not appear to change over the period examined. Percent empty body weight contributed by either the muscle or the bone tissue of the half carcass also did not appear to change. The contribution by the fatty tissue of the half carcass was found to decrease significantly, however ($r = -0.75$, $P < 0.002$).

Since the weight of the empty body is known to be decreasing over the study period, the increase in the percentage contribution to it by the head is probably an indication that the head loses little or no weight over that period (the alternative explanation, that the jaw bone, and possibly other parts of the head continue to grow over the winter is possible, but considering the age of the sampled hinds, it is unlikely that this would result in a weight gain sufficiently large to be detected by the crude form of analysis being employed here).

The increase found in the percentage empty body weight contributed by the empty gut presumably is an indication that the gut does not lose weight over this period, or does so only slightly. However, although the empty body weights of the last nine hinds collected (over the period 29 March to 25 May) are seen to be dropping significantly, the actual weights of the guts of these animals were found to increase significantly ($r = 0.67$, $P < 0.05$). It is possible that red deer (like some

cattle), during periods when the quality of herbage is very poor, undergo a physiological adaptation whereby the length of the gut actually increases (presumably because this increases the efficiency of digestion and absorption; the retention time of such poor quality material also increases); the increase in the weight of the empty gut of the last nine hinds may be an indication of such an adaptation.

The increases observed in the percent empty body weight contributed by the lungs and trachea and by the diaphragm presumably indicate that these organs or tissue do not lose weight, or do so only very slightly. It seems logical, in view of their importance to the process of breathing, that these parts of the body are not likely to undergo much change. In fact the gross weights of these parts of the body decreased slightly in the last nine hinds collected, but the decrease was not significant.

The method that has been employed makes it difficult to form an opinion on whether or not the weight contributions of those organs that did not appear to change (the stomach, heart, liver and kidneys) are undergoing weight changes during the studied period. Since the empty body weight is decreasing, that their percent contributions do not change could be taken to indicate that they are also losing weight, at a similar rate. However, the sample size is not large enough for relatively small losses or gains in weight to be detected as significant. The heart weights of the last nine hinds collected appeared to decrease slightly, but this decrease was not significant ($r = -0.32$, $P < 0.1$). Significant decreases were found in the weights of the stomachs ($r = -0.84$, $P < 0.005$), livers ($r = -0.66$, $P < 0.05$), and kidneys ($r = -0.68$, $P < 0.05$) of these hinds, and this may be an indication that

the weights of these organs (or, in some cases, of fat associated with them) of red deer decrease during this part of the winter and spring. However, both liver and kidneys weights are positively correlated with age, and the significant trend downwards in these weights in the last nine hinds may be due simply to the fact that the last two hinds collected are slightly younger than most of the others.

The observation that the percentages of the empty body weight contributed by the butcher's half carcass or by the weights of muscle or bone tissue from it do not appear to change over the study period may also simply indicate that these parts of the body are decreasing at rates similar to that at which is empty body weight itself. The actual weights of the half carcasses did decrease over the period ($r = -0.39$, $P < 0.09$; Figure 4.2). The weights of both muscle and bone tissue were found to decrease non-significantly ($r = -0.26$, $P > 0.1$; and $r = -0.31$, $P > 0.1$, respectively). The fact that these decreases are not significant may indicate simply the variability of them; but alternatively, the drops may be genuinely occurring, but because they are slight, a larger sample would be required to show their significance. Since the weight of protein in the empty body has been estimated to decrease significantly over the period (see Chapter 3), it may be that a decrease in the weight of muscle tissue in the half carcass does occur over this period (see also Chapter 5).

The contribution to the empty body weight by fatty tissue dissected from the half carcass dropped from just over 3% in the first hind collected to around 1.8% in the last hind. Such a drop is expected in view of the disappearance of

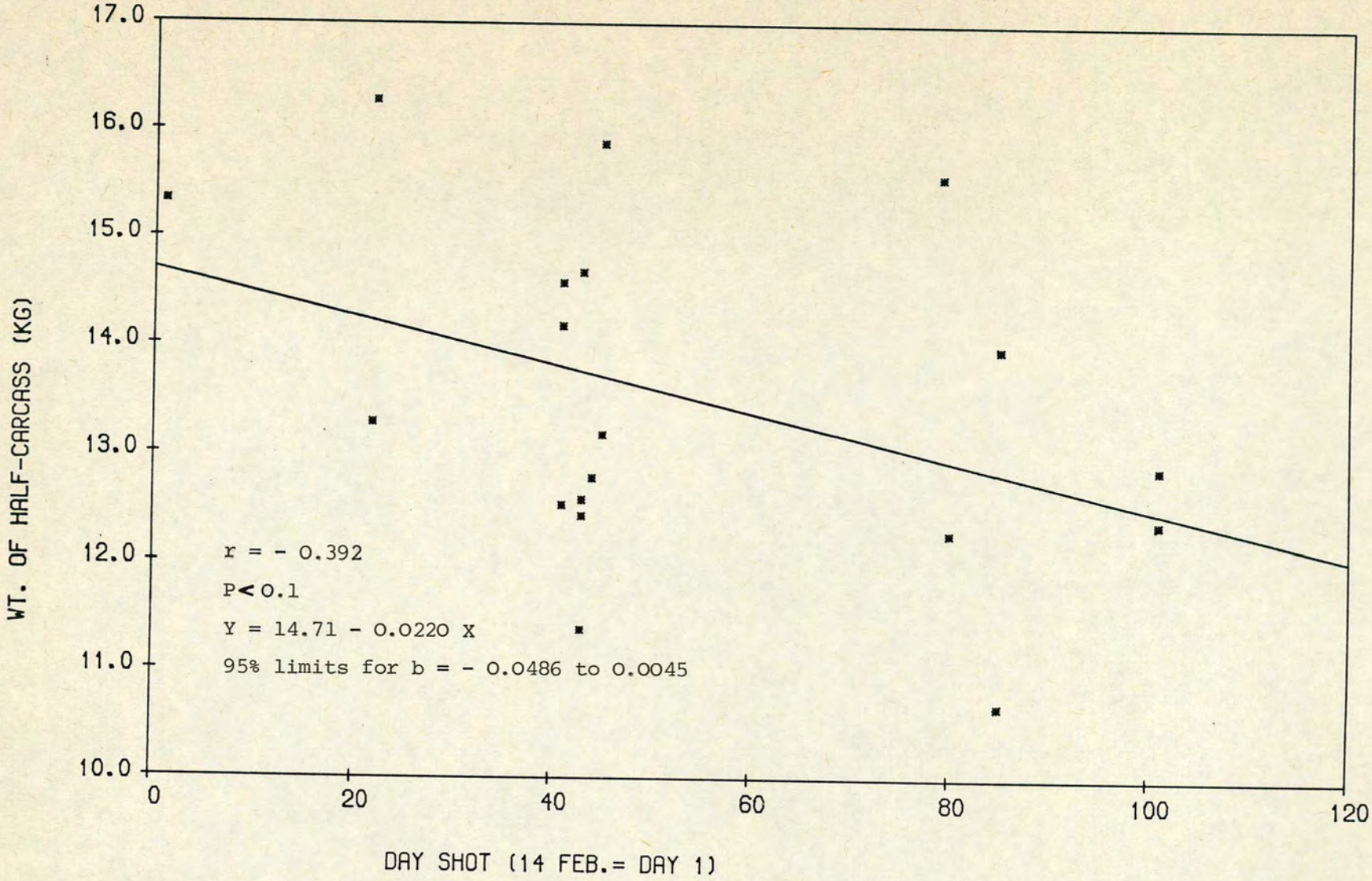


FIG. 4.2. THE DROP IN HALF-CARCASS WEIGHT

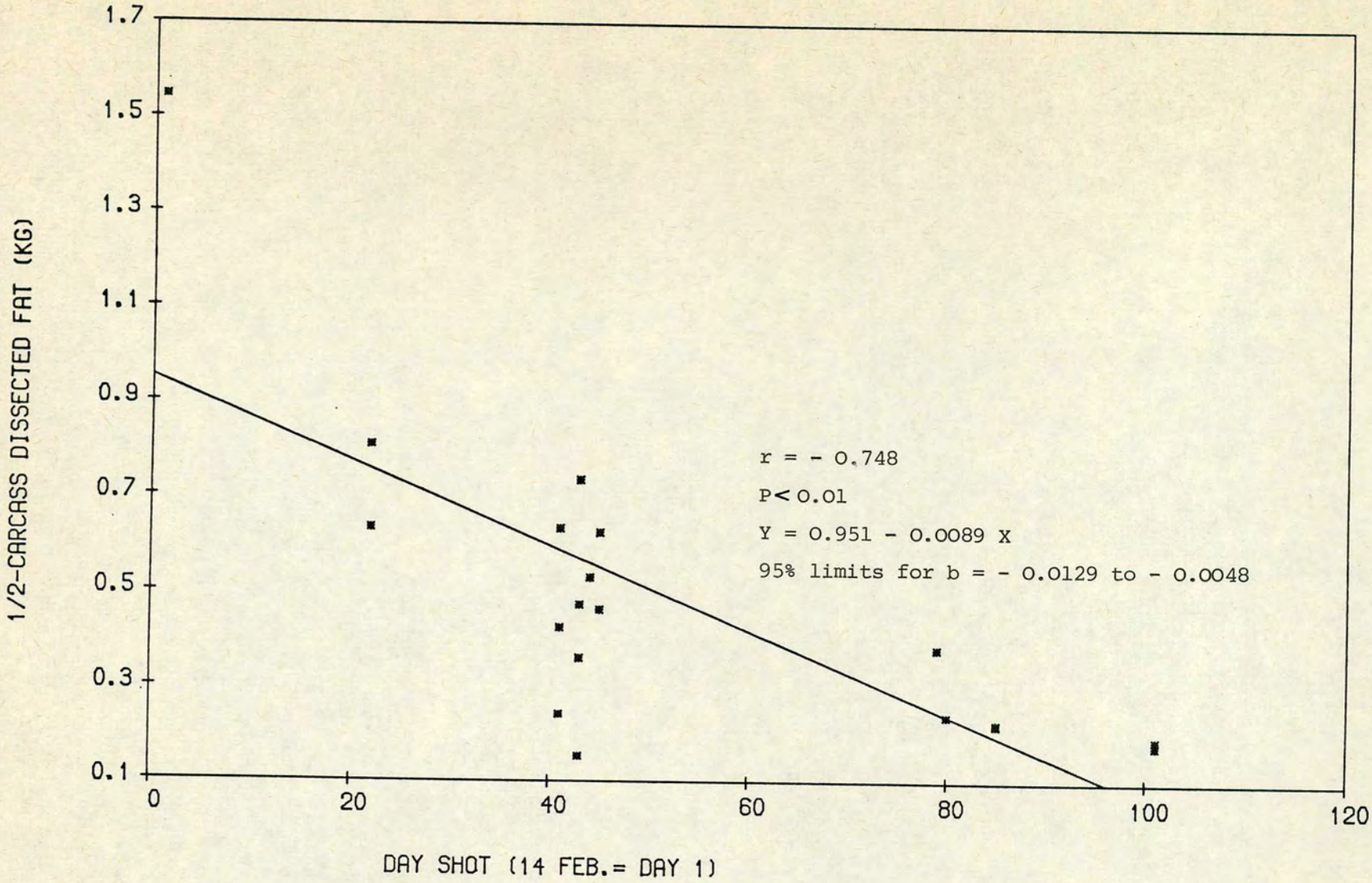


FIG. 4.3. DROP IN DISSECTIBLE FAT WEIGHT

chemically-determined fat from the empty body reported in the last chapter. The weight of fatty tissue dissected from the half carcass was found to decrease from around 1.55 kg to around 0.200 kg (Figure 4.3); this gives an estimated rate of loss of around 9g of dissectible fatty tissue from the half carcass per day over the 100 day period. The estimated rate of loss of chemically-determined fat from the whole empty body, by comparison, is about 50g per day.

4.3. Changes in body conformation as indicated by weight changes of the parts.

The loss of weight from the empty bodies of the hind sample was accompanied by the occurrence of very slight but statistically significant changes in the conformations of the half carcass, and hence the empty body itself. The major change was in the percentage of the empty body weight contained in the offal portion of the body (the head, pelt and internal organs). The offal portion was found to increase by about 6%, from 27 to 33% of the empty body weight. ($r = 0.53$, $P < 0.02$).

The percentage of the empty body weight contributed by the haunch (hind quarter) increased slightly, from 11 to 12.7% ($r = 0.55$, $P < 0.02$). The contribution by the shoulder was found to decrease non-significantly, but that by the loin ($r = -0.56$, $P < 0.02$) decreased very slightly (by 0.5%) but significantly. The contribution by the ribs also decreased very slightly (by 0.8%), and this decrease also was significant ($r = -0.64$, $P < 0.005$). Thus, at the beginning of the study period, the empty body weight of hind 17 was made up approximately as follows:

offal, 27%; hindquarters, 22%; forequarters, 22%; loin, 6%, & ribs, 6%.

By the end of the period, this had changed in hind 35 to: offal, 33%; hindquarters, 26%; forequarters, 21%; loin, 4.5%; & ribs, 5%.

The actual weight of the haunch decreased slightly and non-significantly over the collection period. The weights of the shoulder, loin and ribs all significantly decreased (Figure 4.4). The estimated rate of loss from the shoulder was about 11.8g per day; from the loin around 4.9g per day; and from the ribs, around 6.2g per day.

4.4. Tissue changes occurring within the half carcass. (Table 4.5).

The percentage of the half carcass which is contributed by muscle or bone tissue weight was not found to change significantly over the study period. The percent weight of the half carcass which is fatty tissue decreased from around 6.4% to only about 0.7% ($r = -0.75$, $P < 0.001$). As pointed out before, this represents an estimated loss of around 9g of fatty tissue from the half carcass per day.

4.5. Tissue changes occurring within different areas of the half carcass.

4.5.1. THE HAUNCH (Table 4.6).

There was no indication that the proportion of the haunch which is muscle or bone tissue changed significantly over the study period. The average proportion of muscle tissue was around 80% (4.6 kg), while that of bone was around 16% (0.9 kg). The percentage weight of fatty tissue decreased from around 6% to about 2% ($r = -0.70$, $P < 0.001$); from the actual loss of fatty tissue observed it is estimated that the rate of loss over the period is about 2.5g per day.

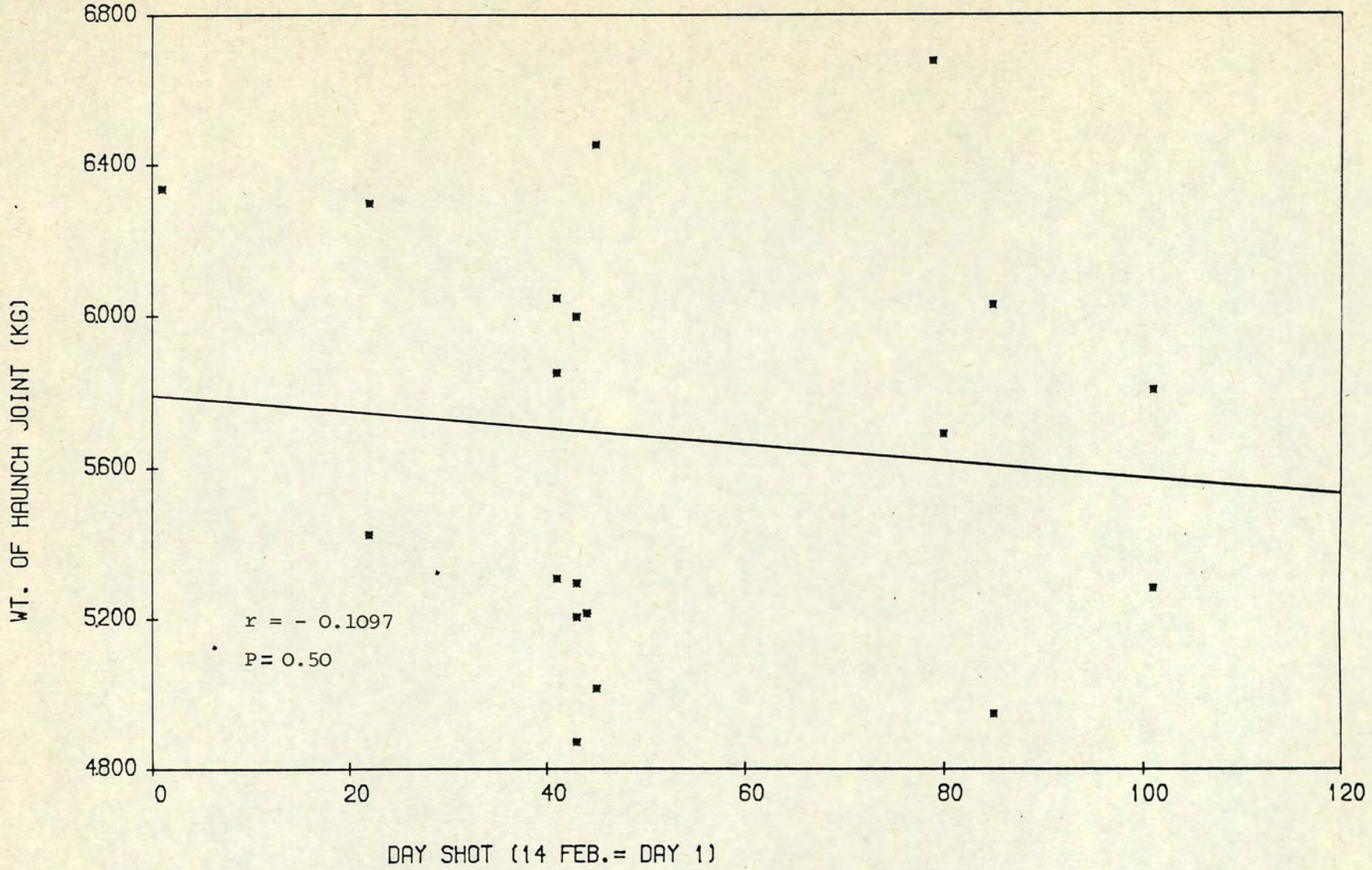


FIG. 4.4(A): DROP IN HAUNCH JOINT WEIGHTS

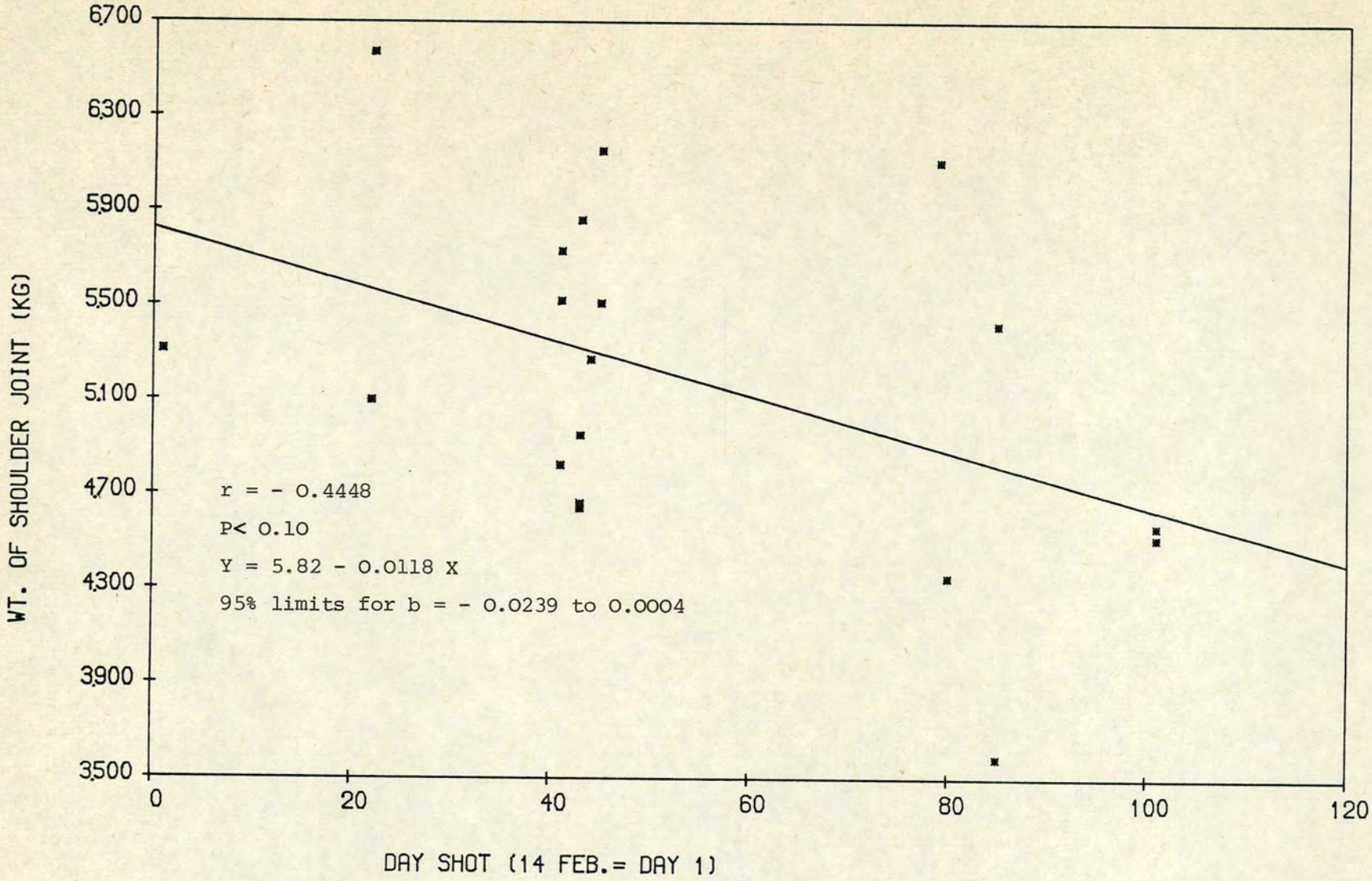


FIG. 4.4(B). DROP IN SHOULDER JOINT WEIGHTS

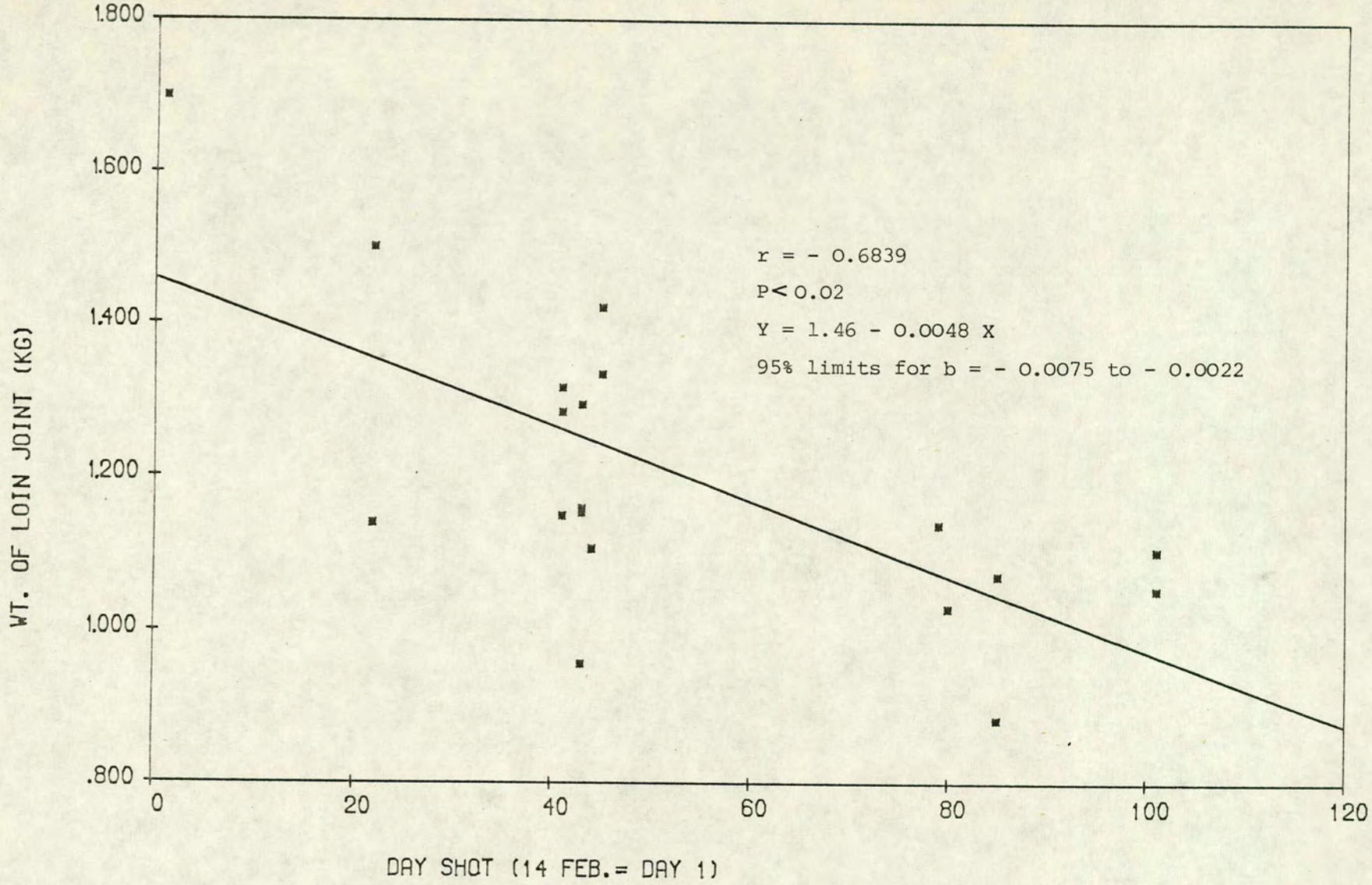


FIG. 4.4(C): DROP IN LOIN JOINT WEIGHTS

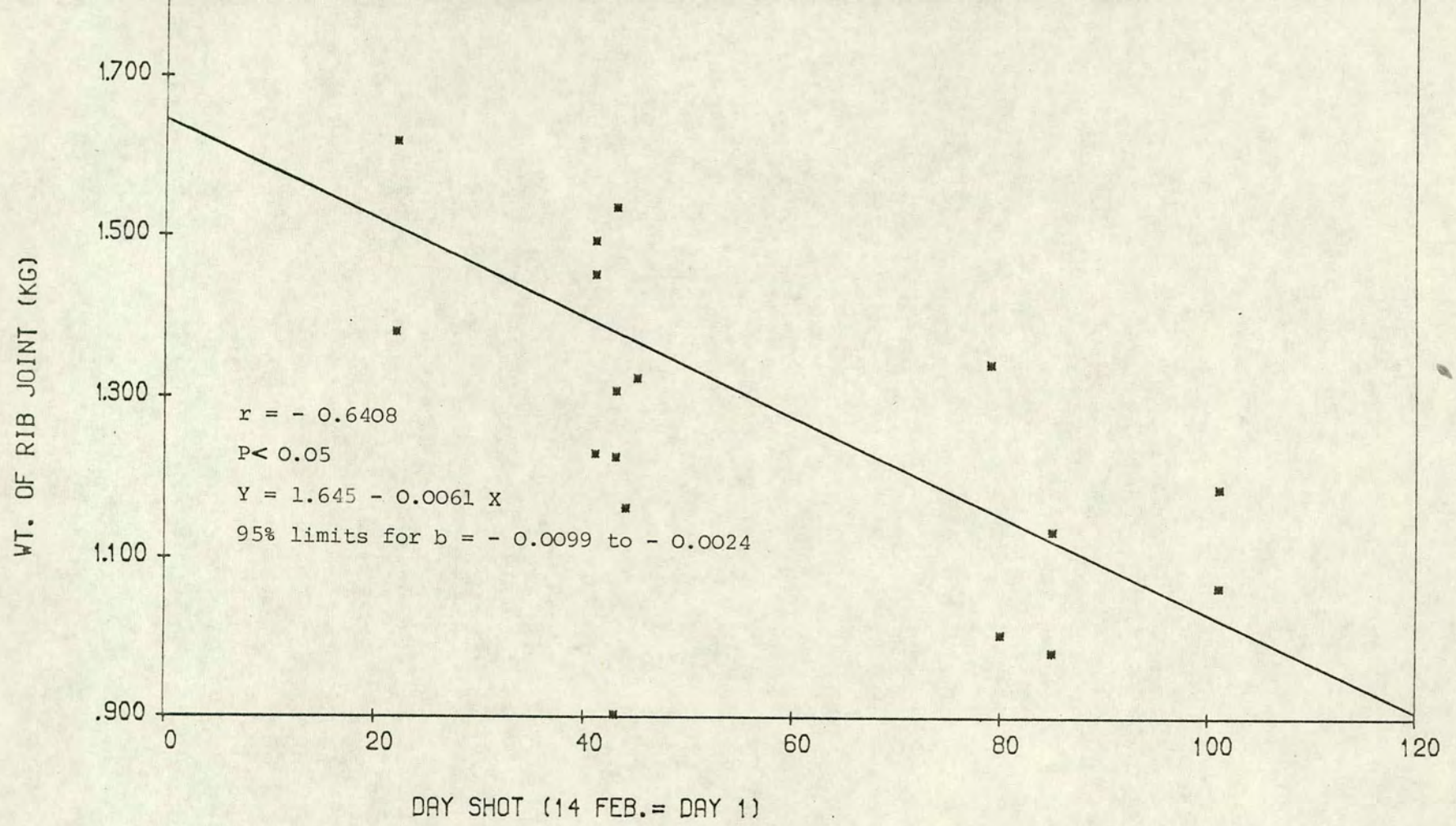


FIG. 4.4(D). DROP IN RIB JOINT WEIGHTS

HIND NUMBER	1/2CARCASS MUSCLE(KG)	1/2CARCASS MUSCLE(%)	1/2CARCASS BONE (KG)	1/2CARCASS BONE (%)
17.0000	11.2820	73.4409	2.4520	15.9615
18.0000	9.2580	69.6090	2.6840	20.1804
19.0000	11.2800	69.2025	3.4060	20.8957
20.0000	10.0240	79.8725	2.1860	17.4183
21.0000	11.1620	76.4520	2.6380	18.0685
22.0000	11.1760	78.7042	2.4560	17.2958
23.0000	9.8600	79.1968	2.3620	18.9719
24.0000	11.2460	76.5034	2.8260	19.2245
25.0000	8.3380	73.1403	2.5420	22.2982
26.0000	9.2300	73.2540	2.4840	19.7143
27.0000	9.5380	74.5156	2.5900	20.2344
28.0000	9.4860	71.8636	3.2040	24.2727
29.0000	12.2460	77.0189	2.8960	18.2138
30.0000	11.9480	76.5897	2.8640	18.3590
31.0000	9.3480	76.0000	2.3580	19.1707
32.0000	7.9820	74.5981	2.1120	19.7383
33.0000	10.5540	75.3857	2.7780	19.8428
34.0000	9.2940	74.9516	2.4400	19.6774
35.0000	10.0320	77.7674	2.2860	17.7209

HIND NUMBER	1/2CARCASS FAT (KG)	1/2CARCASS FAT (%)
17.0000	1.5500	10.0898
18.0000	0.6380	4.7970
19.0000	0.8120	4.9816
20.0000	0.2480	1.9761
21.0000	0.6380	4.3699
22.0000	0.4300	3.0282
23.0000	0.1580	1.2691
24.0000	0.3660	2.4898
25.0000	0.4780	4.1930
26.0000	0.7400	5.8730
27.0000	0.5360	4.1875
28.0000	0.4680	3.5455
29.0000	0.6300	3.9623
30.0000	0.3880	2.4872
31.0000	0.2460	2.0000
32.0000	0.2280	2.1308
33.0000	0.2300	1.6429
34.0000	0.1980	1.5968
35.0000	0.1860	1.4419

Table 4.5. The weights of dissected muscle, bone and fatty tissues from the half carcasses of the collected hinds, and their contributions (%) to half carcass weight.

HIND NUMBER	HAUNCH MUSCLE (G)	MUSCLE % OF HAUNCH WEIGHT	HAUNCH BONE (G)	BONE % OF HAUNCH WEIGHT
17.0000	5008.0000	78.9905	828.0000	13.0599
18.0000	4346.0000	80.0663	844.0000	15.5490
19.0000	4940.0000	78.4127	1028.0000	16.3174
20.0000	4376.0000	82.3795	780.0000	14.6837
21.0000	4724.0000	78.0826	908.0000	15.0083
22.0000	4790.0000	81.8244	820.0000	14.0075
23.0000	4266.0000	80.4906	894.0000	16.8679
24.0000	4826.0000	80.4065	928.0000	15.4615
25.0000	3808.0000	78.0968	854.0000	17.5143
26.0000	4104.0000	78.7716	816.0000	15.6622
27.0000	4100.0000	78.5441	856.0000	16.3985
28.0000	4306.0000	85.7769	1028.0000	20.4781
29.0000	1502.0000	79.0273	942.0000	14.5911
30.0000	5486.0000	82.1257	1046.0000	15.6587
31.0000	4600.0000	80.8152	910.0000	15.9873
32.0000	3912.0000	78.9984	864.0000	17.4475
33.0000	4876.0000	80.8355	982.0000	16.2798
34.0000	4232.0000	80.0605	888.0000	16.7991
35.0000	4802.0000	82.6791	890.0000	15.3237

HIND NUMBER	HAUNCH FAT (G)	FAT % OF HAUNCH WEIGHT
17.0000	482.0000	7.6025
18.0000	206.0000	3.7951
19.0000	270.0000	4.2857
20.0000	154.0000	2.8991
21.0000	372.0000	6.1488
22.0000	236.0000	4.0314
23.0000	110.0000	2.0755
24.0000	164.0000	2.7324
25.0000	204.0000	4.1838
26.0000	250.0000	4.7985
27.0000	162.0000	3.1035
28.0000	168.0000	3.3466
29.0000	380.0000	9.0946
30.0000	138.0000	2.0659
31.0000	140.0000	2.4596
32.0000	126.0000	2.5444
33.0000	130.0000	2.1552
34.0000	126.0000	2.3837
35.0000	124.0000	2.1350

Table 4.6. The weights of dissected muscle, bone and fatty tissues in the whole haunch joint (haunch prime + shank), and their contributions (%) to total haunch weight.

4.5.2. THE SHOULDER AND NECK (Table 4.7).

As in the haunch, there was no indication that the proportion of the shoulder and neck which are muscle or bone tissue changed over the study period. The average percentage of muscle tissue was around 66% (3.8 kg), while that of bone was around 22% (1.4 kg). The percentage weight of fatty tissue here also decreased; in this case from around 5% to around 3.5% ($r = -0.68$, $P < 0.002$). Fatty tissue in the shoulder and neck was estimated to be decreasing in weight at a rate of about 3g per day.

4.5.3. THE LOIN (Table 4.8).

Unlike the apparent lack of change in the muscle of the haunch or shoulder and neck, the percentage of the loin weight which was muscle significantly increased over the study period ($r = 0.46$, $P < 0.05$). However, the actual weight of muscle in the loin of the half carcass samples at the same time underwent a significant decrease ($r = -0.50$, $P < 0.05$); the estimated rate of loss over the period was around 2.6g per day. Furthermore, although the percentage loin weight that was bone did not appear to change, the actual weight of bone tissue also significantly decreased ($r = -0.53$, $P < 0.02$), at an estimated rate of around 2.6g per day. The percentage weight of fatty tissue in the loin weight also significantly decreased ($r = -0.45$, $P < 0.1$); the estimated rate of loss from the loin was around 1g per day.

4.5.4. THE RIBS (Table 4.9).

Apparent tissue change in the ribs was found to be similar to that of the loin. While the percentage of ribs weight which was muscle was not significantly correlated

Table 4.7. The weights of dissectible muscle, bone and fatty tissues in the whole shoulder (shoulder prime, shank and neck), and their contributions (%) to weight of the joint.

HIND NUMBER	WEIGHT OF SHOULDER MUSCLE(G)	SHOULDER % MUSCLE	WEIGHT OF SHOULDER BONE (G)	SHOULDER % BONE
17.0000	3892.0000	73.1579	1064.0000	20.0000
18.0000	3648.0000	71.4453	1196.0000	23.4234
19.0000	4186.0000	63.6170	1558.0000	23.6778
20.0000	3704.0000	76.6239	1006.0000	20.8109
21.0000	4336.0000	75.5401	1224.0000	21.3240
22.0000	4234.0000	76.5642	1132.0000	20.4702
23.0000	3694.0000	79.1006	958.0000	20.5139
24.0000	4388.0000	74.7530	1264.0000	21.5332
25.0000	3268.0000	70.3098	1206.0000	25.9466
26.0000	3484.0000	70.2419	1030.0000	20.7661
27.0000	3812.0000	72.1970	1272.0000	24.0909
28.0000	3450.0000	62.5000	1358.0000	24.6014
29.0000	4662.0000	75.6327	1300.0000	21.0902
30.0000	4558.0000	74.4771	1320.0000	21.5686
31.0000	3300.0000	75.6881	1002.0000	22.9816
32.0000	2692.0000	74.8609	822.0000	22.8587
33.0000	4056.0000	74.6961	1302.0000	23.9779
34.0000	3412.0000	75.3533	1068.0000	23.5866
35.0000	3540.0000	77.3601	984.0000	21.5035

) GO :

WEIGHT OF SHOULDER FAT (G)	SHOULDER % FAT
328.0000	6.1654
196.0000	3.8386
284.0000	4.3161
88.0000	1.8204
114.0000	1.9861
134.0000	2.4231
0.0000	0.0000
164.0000	2.7939
174.0000	3.7435
348.0000	7.0161
166.0000	3.1439
172.0000	3.1159
174.0000	2.8228
204.0000	3.3333
36.0000	0.8257

Table 4.8. The weights of dissectible muscle, bone and fatty tissues in the loin joint, and their contributions (%) to weight of the joint.

HIND NUMBER	WEIGHT OF LOIN MUSCLE(G)	% LOIN MUSCLE	WEIGHT OF LOIN BONE(G)	% LOIN BONE
17.0000	1156.0000	67.9201	234.0000	13.7485
18.0000	852.0000	74.6059	232.0000	20.3152
19.0000	1130.0000	75.1330	306.0000	20.3457
20.0000	986.0000	85.5903	146.0000	12.6736
21.0000	1022.0000	79.4712	156.0000	12.1306
22.0000	1114.0000	84.5220	168.0000	12.7466
23.0000	932.0000	80.6228	180.0000	15.5709
24.0000	974.0000	75.1543	264.0000	20.3704
25.0000	694.0000	72.2917	212.0000	22.0833
26.0000	838.0000	72.1170	252.0000	21.6867
27.0000	852.0000	76.7567	156.0000	14.0541
28.0000	954.0000	71.4072	344.0000	25.7485
29.0000	1178.0000	82.7247	208.0000	14.6067
30.0000	954.0000	83.5376	144.0000	12.6095
31.0000	846.0000	81.8182	146.0000	14.1199
32.0000	688.0000	77.4775	148.0000	16.6667
33.0000	856.0000	79.5539	178.0000	16.5427
34.0000	802.0000	75.8034	178.0000	16.8242
35.0000	940.0000	84.8375	140.0000	12.6354

HIND NUMBER	WEIGHT OF LOIN FAT (G)	LOIN % FAT
17.0000	304.0000	17.8613
18.0000	46.0000	4.0280
19.0000	20.0000	1.3298
20.0000	0.0001	0.0000
21.0000	94.0000	7.3095
22.0000	30.0000	2.2762
23.0000	38.0000	3.2872
24.0000	34.0000	2.6235
25.0000	46.0000	4.7917
26.0000	56.0000	4.8193
27.0000	86.0000	7.7477
28.0000	38.0000	2.8443
29.0000	28.0000	1.9663
30.0000	24.0000	2.1016
31.0000	24.0000	2.3211
32.0000	26.0000	2.9279
33.0000	40.0000	3.7175
34.0000	54.0000	5.1040
35.0000	6.0000	0.5415

GO :

Table 4.9. The weights of dissectible muscle, bone and fatty tissues in the ribs joint, and their contributions (%) to the weight of the joint.

HIND NUMBER	WEIGHT OF RIBS MUSCLE(G)	MUSCLE IN RIBS (%)	WEIGHT OF RIBS BONE (G)	BONE IN RIBS (%)
17.0000	1226.0000	65.9140	326.0000	17.5269
18.0000	904.0000	65.3179	412.0000	29.7688
19.0000	1024.0000	63.1319	514.0000	31.6893
20.0000	958.0000	77.6337	254.0000	20.5835
21.0000	1080.0000	72.0961	350.0000	23.3645
22.0000	1038.0000	71.2912	336.0000	23.0769
23.0000	968.0000	73.7805	330.0000	25.1524
24.0000	1058.0000	68.7013	370.0000	24.0260
25.0000	568.0000	62.6931	270.0000	29.8013
26.0000	804.0000	65.3658	386.0000	31.3821
27.0000	774.0000	66.3808	306.0000	26.2436
28.0000	776.0000	58.4337	474.0000	35.6928
29.0000	1304.0000	71.8853	446.0000	24.5865
30.0000	950.0000	70.5795	354.0000	26.3001
31.0000	602.0000	59.7222	300.0000	29.7619
32.0000	690.0000	69.9797	278.0000	28.1947
33.0000	766.0000	67.3111	316.0000	27.7680
34.0000	848.0000	71.1409	306.0000	25.6711
35.0000	750.0000	70.2247	272.0000	25.4682

WEIGHT OF RIBS FAT (G)	RIBS FAT (%)
296.0000	15.9140
52.0000	3.7572
60.0000	3.6991
6.0000	0.4862
58.0000	3.8718
30.0000	2.0604
10.0000	0.7622
4.0000	0.2597
54.0000	5.9603
30.0000	2.4390
58.0000	4.9743
60.0000	4.5181
48.0000	2.6461
22.0000	1.6345
46.0000	4.5635
8.0000	0.8114
44.0000	3.8664
18.0000	1.5101
34.0000	3.1835

29 GO :

with time, the weight of muscle in the ribs portions of the half carcasses significantly decreased ($r = -0.53$, $P < 0.02$) at an estimated rate of around 4g per day. The percentage weight of bone also did not appear to change significantly, but the weight of bone in the ribs was found to decrease ($r = -0.44$, $P < 0.1$) at an estimated rate of around 1g per day. As in all the other areas of the half carcass, the percentage ribs weight that was fatty tissue significantly decreased ($r = -0.46$, $P < 0.05$), disappearing at a rate estimated at around 1g per day.

4.6. A summary of the tissue changes occurring in the half carcass over the late winter and spring.

4.6.1.

The butcher's half carcasses of the collected hinds were found to decrease significantly in weight over the period examined ($r = -0.39$, $P < 0.1$). The lack of a significant correlation between age of the hinds and the dates when they were shot suggests that the decrease in weight of the half carcasses of the sample population is an indication that the equivalent portion of the bodies of wild hinds tends to decrease similarly over the late winter and spring period. The estimated rate of loss from the half carcass was around 22g per day, but the high variability in half carcass weights of the sample, resulting in the correlation between time and weight being significantly only at the 10% level, suggests that this figure should be accepted only as a rough indication of the size of the average weight loss occurring.

4.6.2.

The relationships between time and the weights of muscle tissues contained in the different areas of the half carcass, when the weight of muscle in a particular joint is expressed

as a percentage of the muscle weight of the whole of the half carcass, were found to be of considerable interest. No significant relationship was found between time and the percentage of muscle tissue located in the shoulder and neck (considered as one unit). However, the percentages in the loin and in the ribs significantly decreased ($r = -0.59$, $P < 0.01$; and $r = -0.59$, $P < 0.01$, respectively), while that in the haunch increased ($r = 0.57$, $P < 0.02$; see Table 4.10). Such results can be indications either that

a) the weight of muscle in the haunch is increasing, while that in the shoulder does not change, and the loin and ribs also do not change, or decrease, or even increase, but at a slower rate to that in the haunch; or that

b) the weight of the haunch muscle and shoulder muscle are more or less constant while those of the loin and ribs are decreasing; or that

c) the weights of muscle in all areas are decreasing, but that of the haunch at a slower rate, and that of the loin and of the ribs at a faster rate, than is the shoulder. In fact the weight of muscle in the whole of the half carcass was found to decrease, although non-significantly, over the study period, which would seem to suggest that it is most likely that the weight of muscle in the haunch does not increase (case b or c), and that the decreases observed in the loin and the ribs are indications of genuine trends which occur in wild hinds over the period examined.

The percentages of total half carcass bone weight contained in the different areas were found to vary in the same fashion as did the percentages of muscle weights (Table 4.11). Percent shoulder and neck bone showed no significant change with time, while those of both the loin and the ribs decreased ($r = -0.55$, $P < 0.02$; and $r = -0.45$, $P < 0.1$, respectively);

HIND NUMBER	% MUSCLE LOCATED IN HAUNCH	% MUSCLE LOCATED IN SHOULDER	% MUSCLE LOCATED IN LOIN	% MUSCLE LOCATED IN THE RIBS
17.0000	44.3890	34.4970	10.2460	10.8670
18.0000	46.9400	39.4000	9.2000	9.7600
19.0000	43.7900	37.1100	10.0200	9.0800
20.0000	43.6600	36.9500	9.8400	9.5600
21.0000	42.3200	38.8400	9.1600	9.6800
22.0000	42.3600	37.8800	9.9700	9.2900
23.0000	43.2600	37.4600	9.4500	9.8200
24.0000	42.9100	39.0200	8.6600	9.4100
25.0000	45.6700	39.1900	8.3200	6.8100
26.0000	44.4600	37.7500	9.0800	8.7100
27.0000	42.9900	39.9700	8.9300	8.1100
28.0000	45.3900	36.3700	10.0600	8.1800
29.0000	41.6600	38.0700	9.6200	10.6500
30.0000	45.9200	38.1500	7.9800	7.9500
31.0000	49.2100	35.3000	9.0500	6.4400
32.0000	49.0100	33.7200	8.6200	8.6400
33.0000	46.2000	38.4300	8.1100	7.2600
34.0000	45.5300	36.7100	8.6300	9.1200
35.0000	47.8700	35.2900	9.3700	7.4800

Table 4.10. The percentages of the total dissectible muscle weight located in the four main joints.

Table 4.11.(below) The percentages of total half carcass dissectible bone weight located in the four major joints.

HIND NUMBER	% BONE LOCATED IN THE HAUNCH	% BONE LOCATED IN SHOULDER	% BONE LOCATED IN THE LOIN	% BONE LOCATED IN THE RIBS
17.0000	33.7700	43.3900	9.5400	13.3000
18.0000	31.4400	44.5600	8.6400	15.3500
19.0000	30.1800	45.7200	8.9800	15.0900
20.0000	35.6800	46.0200	6.6800	11.6200
21.0000	34.4200	46.4000	5.9300	13.2700
22.0000	33.3900	46.0900	6.8400	13.6800
23.0000	37.8500	40.5600	7.6200	13.9700
24.0000	32.8400	44.7300	9.3400	13.0900
25.0000	33.6000	47.4400	8.3400	10.6200
26.0000	32.8500	41.4600	10.1400	15.5400
27.0000	33.0500	49.1100	6.0200	11.8100
28.0000	32.0800	42.3800	10.7400	14.7900
29.0000	32.5300	44.8900	7.1800	15.4000
30.0000	36.5200	46.0900	5.0300	12.3600
31.0000	38.5900	42.4900	6.1900	12.7200
32.0000	40.9100	38.9200	7.0100	13.1600
33.0000	35.3500	46.8700	6.4100	11.3800
34.0000	36.3900	43.7700	7.3000	12.5400
35.0000	38.9200	43.0400	6.1200	11.9000

HIND NUMBER	% CARCASS FAT IN HAUNCH	% CARCASS FAT IN SHOULDER	% CARCASS FAT IN THE LOIN	% CARCASS FAT IN THE RIBS
17.0000	31.0900	21.1600	19.6200	19.1000
18.0000	32.2900	30.7200	7.2100	8.1500
19.0000	33.2500	34.9800	2.4600	7.3900
20.0000	62.1000	35.4800	0.0000	2.4200
21.0000	58.3100	17.8700	14.7300	9.0900
22.0000	54.8800	31.1600	6.9800	6.9800
23.0000	69.6200	0.0000	24.0500	6.3300
24.0000	44.8100	44.8100	9.2900	1.0900
25.0000	42.6800	36.4000	9.6200	11.3000
26.0000	33.7800	42.0700	7.5700	4.0500
27.0000	30.2200	30.9700	16.0400	10.8200
28.0000	35.9000	36.7500	8.1200	12.8200
29.0000	60.3200	27.6200	4.4400	7.6200
30.0000	35.5700	52.5800	6.1800	5.6700
31.0000	56.9100	14.6300	9.7600	18.7000
32.0000	55.2600	29.8200	11.4000	3.5100
33.0000	56.5200	6.9600	17.3900	19.1300
34.0000	63.6400	0.0000	27.2700	9.0900
35.0000	66.6600	11.8300	3.2200	18.2800

Table 4.12.(above) The percentages of half carcass dissectible associated fatty tissue located in the major four joints.

that of haunch bone increased ($r = 0.72$, $P < 0.001$). The possible explanations for these findings are the same as were offerred for the changes in muscle tissue distribution. Again, the weight of haunch bone in the half carcass was negatively though non-significantly correlated with time, and I think it likely that haunch bone does not increase in weight over the study period. The decreases occurring in the percentage total bone found in the loin and in the ribs again suggest that weight losses probably do occur in the bones of these areas during the period mid-February to June. Unfortunately, the sample was too small for one to be able to say whether this loss is due simply to the loss of bone marrow fat, or whether minerals of the bone itself are also being mobilised and thus lost during this period.

The situation in relation to fatty tissue distribution throughout the half carcass was different than those of muscle or bone (Table 4.12). The percent total half carcass dissected fat weight (including perirenal fatty tissue) represented by the tissue in the haunch, significantly increased ($r = 0.54$, $P < 0.02$). However, the shoulder, loin and ribs percentages did not appear to change; their average values being 27%, 11% and 10% respectively. The percentage of kidney fat weight in the half carcass tissue significantly decreased ($r = -0.70$, $P < 0.001$). The estimated rate of loss of kidney fat weight was around 1.5g per day.

Regression analysis of half carcass dissected fatty tissue (including the perirenal tissue) against time suggested that fatty tissue was being lost from the half carcass at a rate of around 9g per day. The distribution of this loss appears to have been:

loss from the haunch	=	2.5 g/day;
loss from the shoulder and neck	=	3.0
loss from the loin	=	1.0
loss from the ribs	=	1.0
loss from the perirenal area	=	1.5; so that
total loss of fatty tissue from the half carcass	=	9.0 g/day.

4.6.3.

Neither the expression of muscle and bone tissues within the half carcass as percentages of empty-body weight, nor the weights of the tissues themselves, was able to demonstrate any significant relationship with the passing of time over the study period. Therefore, the finding of significant correlations between time and the percentages of muscle and of bone tissue as located in the different areas of the body is of considerable interest, since it demonstrates that weight changes of these tissues, however slight, are occurring over the late winter/spring period. As has already been pointed out, changes in percentages cannot indicate whether a particular tissue is increasing or decreasing in weight, however.

4.7. Conclusions on tissue weight changes.

Whether the changes in percent distribution of muscle and of bone tissues represent gains or losses in weight, and why they might be occurring, are discussed in detail in the next chapter. Nevertheless, at this point I would like to suggest that the combined evidence of the detailed chemical analyses, the changes in percent distribution, and the observed decreases in tissue weight, indicate that genuine weight losses are occurring in the majority of wild Scottish hinds over the period mid-February to June; and that these

losses are not only of fatty tissue, but also of muscle and of bone tissue, at least within the areas of the loin and the ribs. What the composition of these losses might be, within the tissues, is discussed in the next chapter.

CHAPTER 5. The Effects of Severe Winter Malnutrition on the Bodies of Wild Scottish Red Deer Hinds.

The first objective of the research reported on in this thesis was to establish why wild Scottish red deer hinds undergo the considerable losses in body weight so characteristic of them during the winter and spring. To achieve this goal the sample population of 19 hinds was collected, the only known bias being the selecting for only animals which were pregnant. For that reason the sample included only four milk hinds. However, in the lack of evidence to the contrary, the sample is accepted as being representative of adult (4 to 10 years old) pregnant yeld hinds in the areas from which it was collected, and over the period mid-February to the beginning of June. Furthermore, because of the apparent similarities in vegetation (and hence in dietary energy supply) and in weather (and thus in environmental energy demand), and because of the relative spatial proximity of the two areas, the differences between the deer populations at Glen Feshie and Corrour, and between the environmental factors of their ecosystems which affect the energy status of the deer, are assumed to be relatively minor: the animals collected from these two areas therefore will be considered as representative of a single theoretical population. (For the reasons given in section 2.6 of Chapter 2, the data on the two hinds from Killilan are accepted also as being typical members of this hypothetical population).

5.1. The reason for winter body weight loss.

Because it was not possible to collect animals which were of the same age and original body size and weight, some of the variation found in the various parameters of

the sample population is due simply to differences in these factors, rather than differences experienced in energy or nutritional regimes. However, the dramatic drop observed in gross energy content per unit of body weight strikingly demonstrates how the majority of pregnant adult hinds at Glen Feshie and Corrour must have been in negative energy balance during most or all of the period mid-February to the end of April or May (cf Table 3.8 and Figure 3.5). There should be little doubt that this loss occurred because the metabolic requirements of the hinds for energy, increased during this period by the additional demands made by their developing foetuses and by the weather, could not be met by dietary means, and that they therefore were in a state of severe dietary energy deficiency. It therefore became necessary for them to katabolise fat stored within the tissues of their bodies to meet these requirements. It is this loss of body fat, necessitated by the considerable deficit of dietary energy intake, which appears to be largely responsible for the losses in body weight which occur during winter and spring.

The equation derived from regression analysis of the sampled hinds estimates that energy loss from the empty (ingesta- and conceptus-free) body occurred over the 100 day studied period at the rate of around 8 kcal per kg of empty-body weight per day (see also Chapter 3; section 3.4, and Table 3.8 and Figure 3.5). However, the estimates of gross energy (and all other contents of the empty body as chemically determined) depend upon the determined dry matter (DM) contents of the 100g samples representative of the empty bodies of the hinds. Since these DM determinations are known to be higher than the actual DM content of the

bodies of the animals when they were alive (because of the moisture losses which occurred, mainly during storage), the data from only those hinds which had remained in storage for 150 days or less were examined. The resulting sub-sample population consisted of 11 hinds (numbers 17, 25, 26, 27, 28, 30, 31 and 33 having been withdrawn; see Figure 5.1), covering the period 7 March to 25 May.

The drop in empty-body weight of the sub-sample of 11 hinds was more closely negatively correlated with the passage of time than was that of the whole sample ($r = -0.676$, $P<0.05$; as compared to $r = -0.51$). The derived regression equation estimates that over this period empty-body weight was dropping at a rate of around 116g per day (Figure 5.2); this compared with an estimated rate of loss of around 84g per day over the whole 100 day period from mid-February to the end of May. The loss in gross energy from the empty bodies of the 11 sub-sample hinds is estimated to have been occurring at a slightly slower rate (of around 7 kcal/kg empty-body weight/day; see Figure 5.3).

The correlations (presented in Table 5.1) between variation in gross energy content of the empty body and its weight, and the weights of its major components, appear to be convincing evidence that the loss in empty-body weight found to be occurring is due ultimately to the energy deficiency which the hinds have been seen to be suffering over the studied period. The close relationship between the weight of the empty body and its gross energy content is shown in Figure 5.4. The high correlations between gross energy content, empty-body chemical fat weight and empty-body weight very much support the opinion that the

Table 5.1. Correlation matrix between time and the weights of the major components of the empty body.

	TIME (14 FEB=DAY 1)	EMPTY-BODY WEIGHT (KG)	BODY WATER CONTENT (KG)	EMPTY-BODY PROTEIN WT (KG)	WEIGHT OF BODY FAT (KG)
EMPTY-BODY WEIGHT (KG)	--				
	-0.514				
	2.000%				
	26.4%				
BODY WATER CONTENT (KG)	.	++++++			
	-0.109	0.866			
	70.000%	0.001%			
	1.2%	75.1%			
EMPTY-BODYPROTEIN WT (KG)	------	++++++	++		
	-0.648	0.810	0.535		
	0.000%	0.002%	2.000%		
	42.0%	65.6%	28.6%		
WEIGHT OF BODY FAT (KG)	------	++++++	.	++++++	
	-0.911	0.676	0.262	0.700	
	0.001%	0.000%	30.000%	0.080%	
	83.0%	45.6%	6.9%	49.0%	
EMPTY-BODY ENERGY (MCAL)	-------	++++++	.	++++++	++++++
	-0.836	0.816	0.435	0.799	0.962
	0.001%	0.002%	6.000%	0.004%	0.001%
	69.8%	66.6%	18.9%	63.8%	92.5%

26 GO :

N.B.: -

the first value is r;

the second value is P;

the third value is R^2.

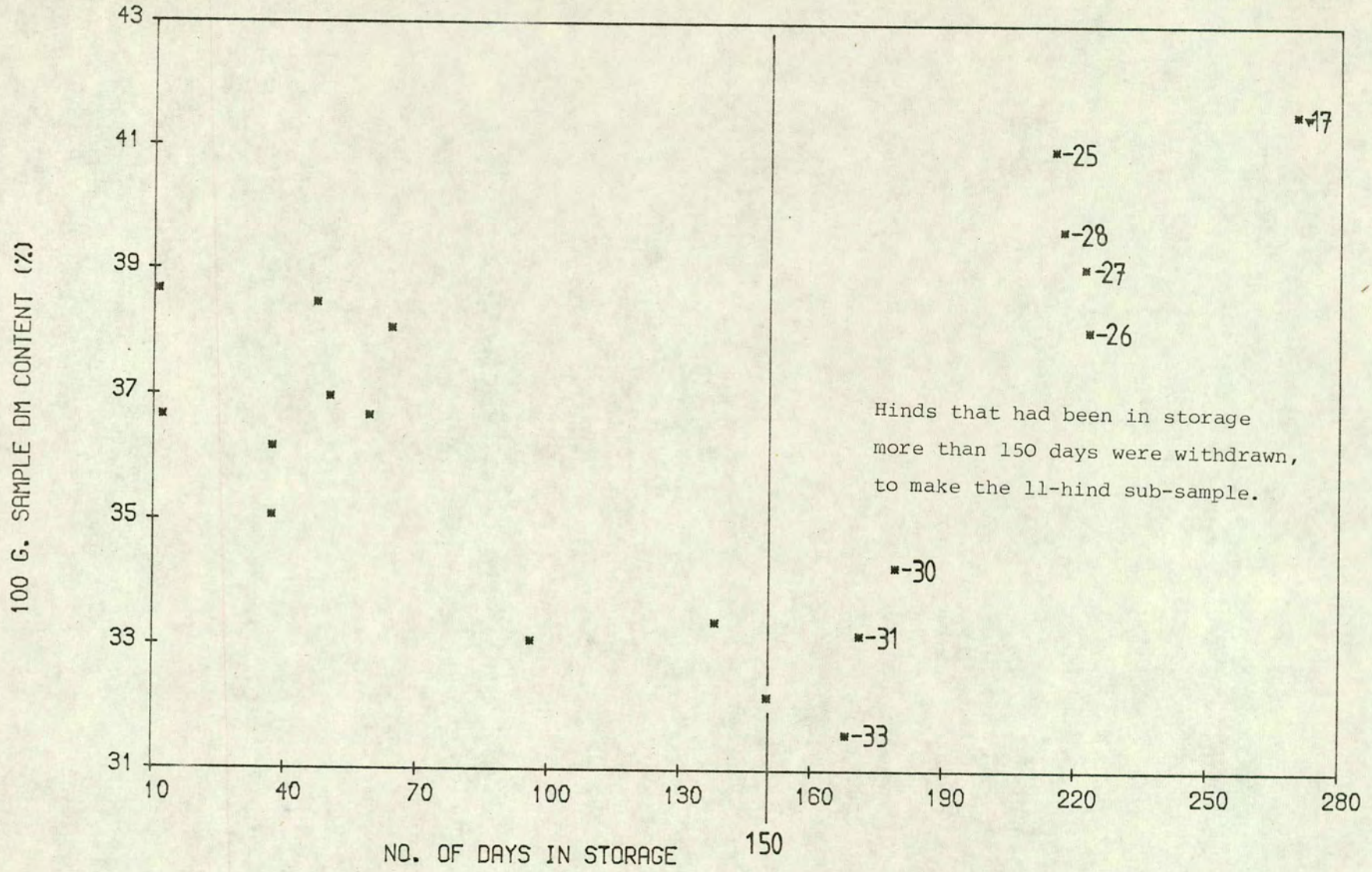


FIG. 5.1. HINDS REMOVED TO MAKE SUB-SAMPLE

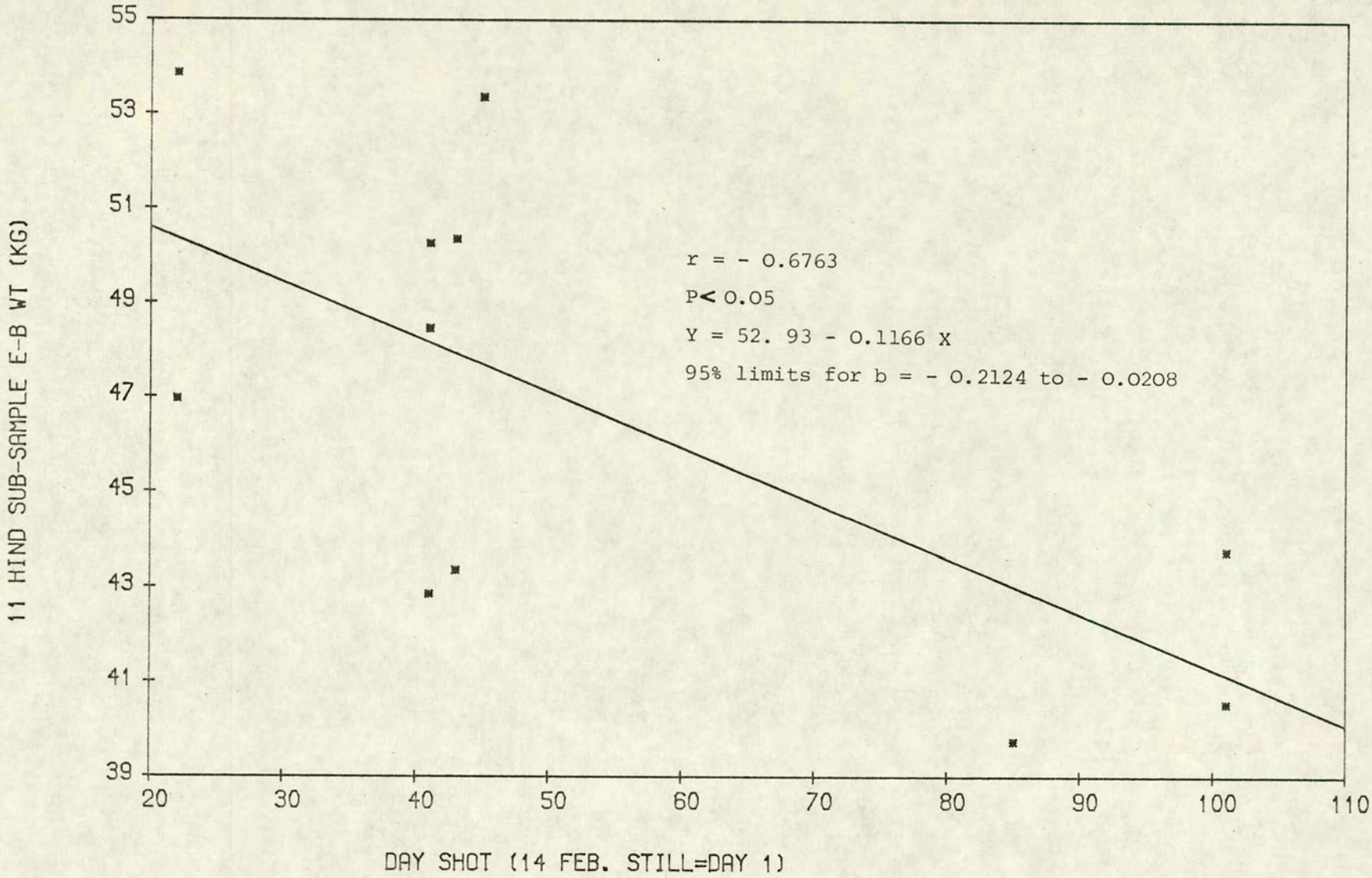


FIG. 5.2. SUB-SAMPLE E-B WT. LOSS

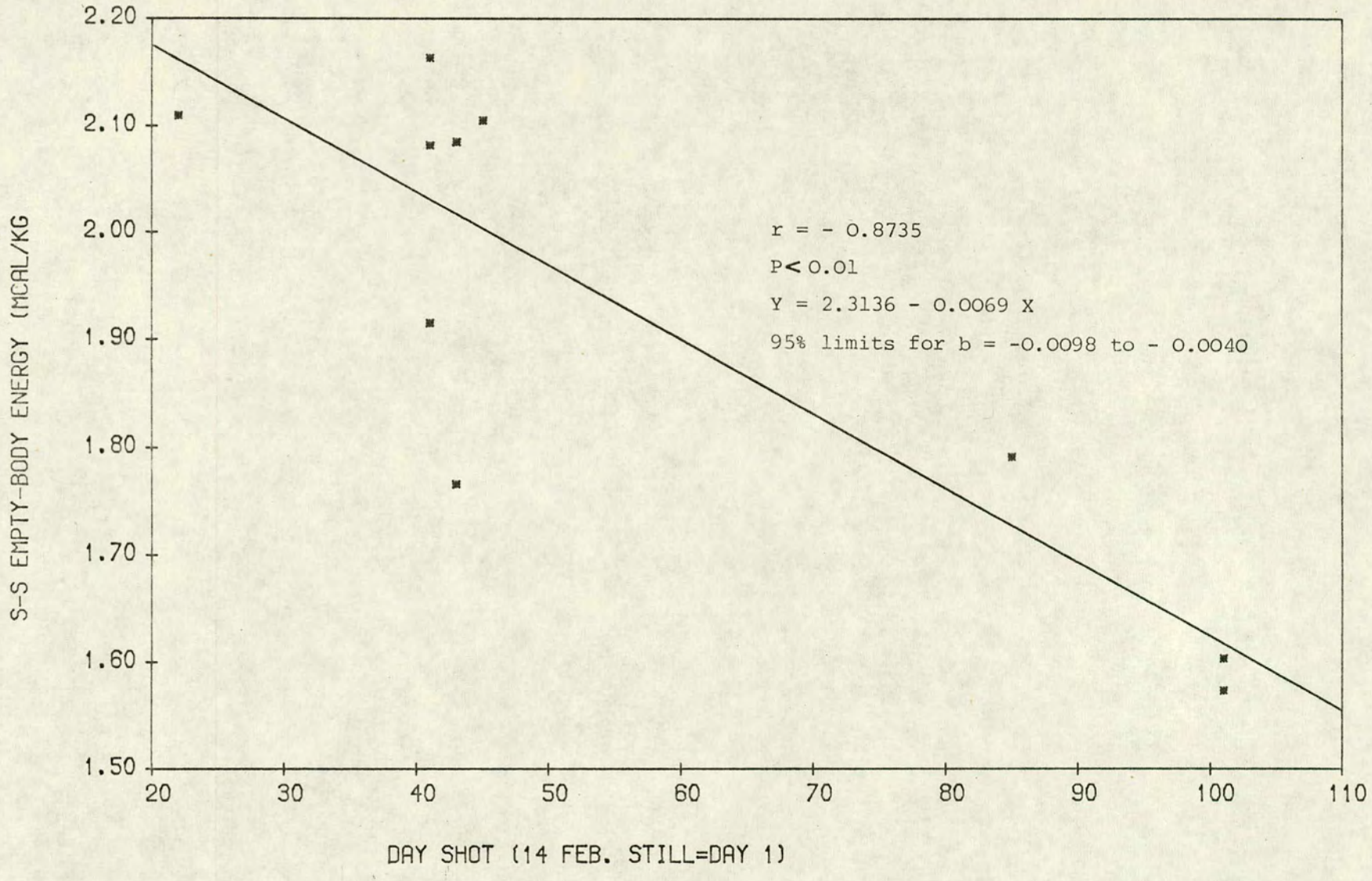


FIG. 5.3. S-S EMPTY-BODY ENERGY LOSS

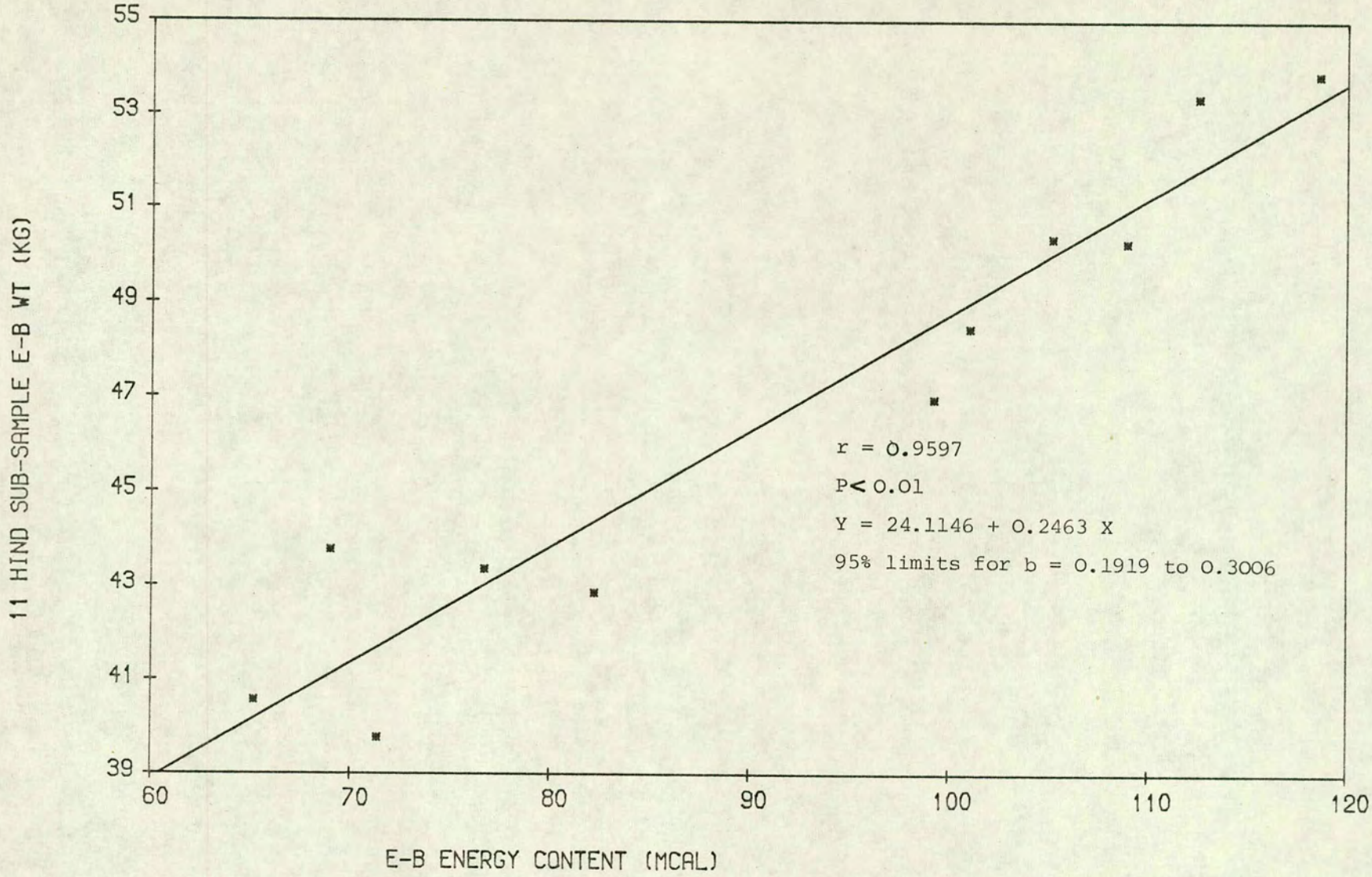


FIG. 5.4. E-B WT. RELATED TO ENERGY CONTENT

major proximate cause of weight loss over this period is the loss of chemical fat. It is particularly striking that, in spite of differences in age, and presumably between individuals, variation in chemical fat weight can explain 79 percent of the variation observed in the weights of the empty bodies of the 11 sub-sample hinds (Figure 5.5). The actual weight of chemical fat lost by these hinds is shown in Figure 5.6.

Although the variation in empty-body weight of the sub-sample hinds has been seen to be most closely correlated to variation in the weight of fat the empty body contains, body weight of course also is affected by the weight of protein present (as shown in Figure 5.7). The fact that variation in body weight is less closely correlated with weight of protein is to be expected, if it be accepted that the major cause of the drop in empty-body weight occurring is due to the loss of fat. However, the weight of protein in the bodies of the sub-sample hinds is also significantly negatively correlated with the passing of time ($r = -0.640$, $P < 0.05$; see Figure 5.8). Thus, although the percentage of nitrogen in the DM of the 100g representative samples significantly increased over the studied period (due to the disappearance of chemical fat: see Chapter 3, section 3.1.4), the actual weight of protein present appears to have decreased. In view of the finding that the age of the hinds was not significantly related to the passing of time, nor is protein weight as highly correlated with age ($r = 0.595$, $P < 0.01$) as it is with the passage of time, this negative correlation is taken to be an indication that protein was being katabolised over the studied period, in addition to fat (the correlation between protein loss and time is marginally even greater for

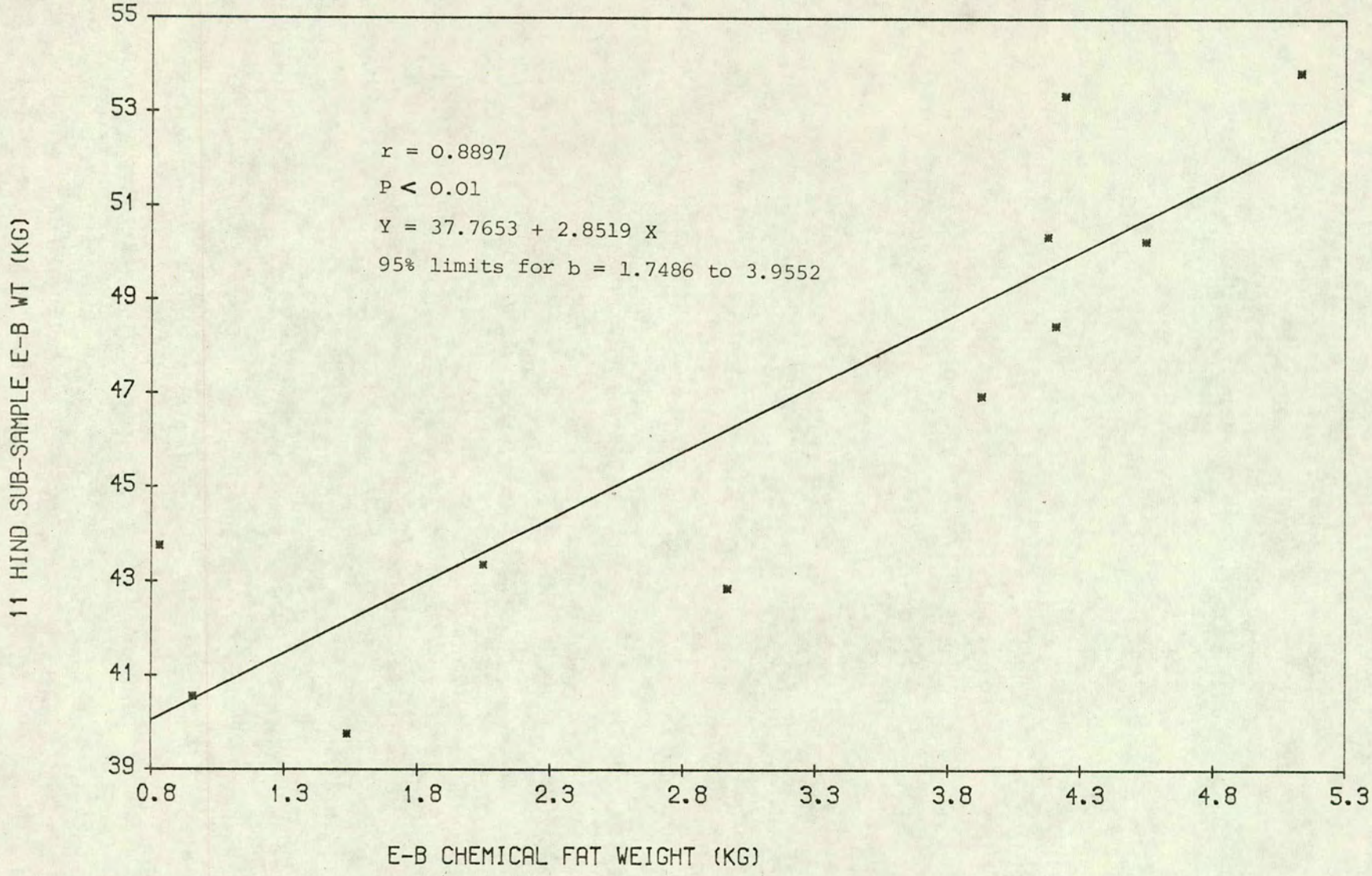


FIG.5.5. E-B WT. RELATED TO FAT CONTENT

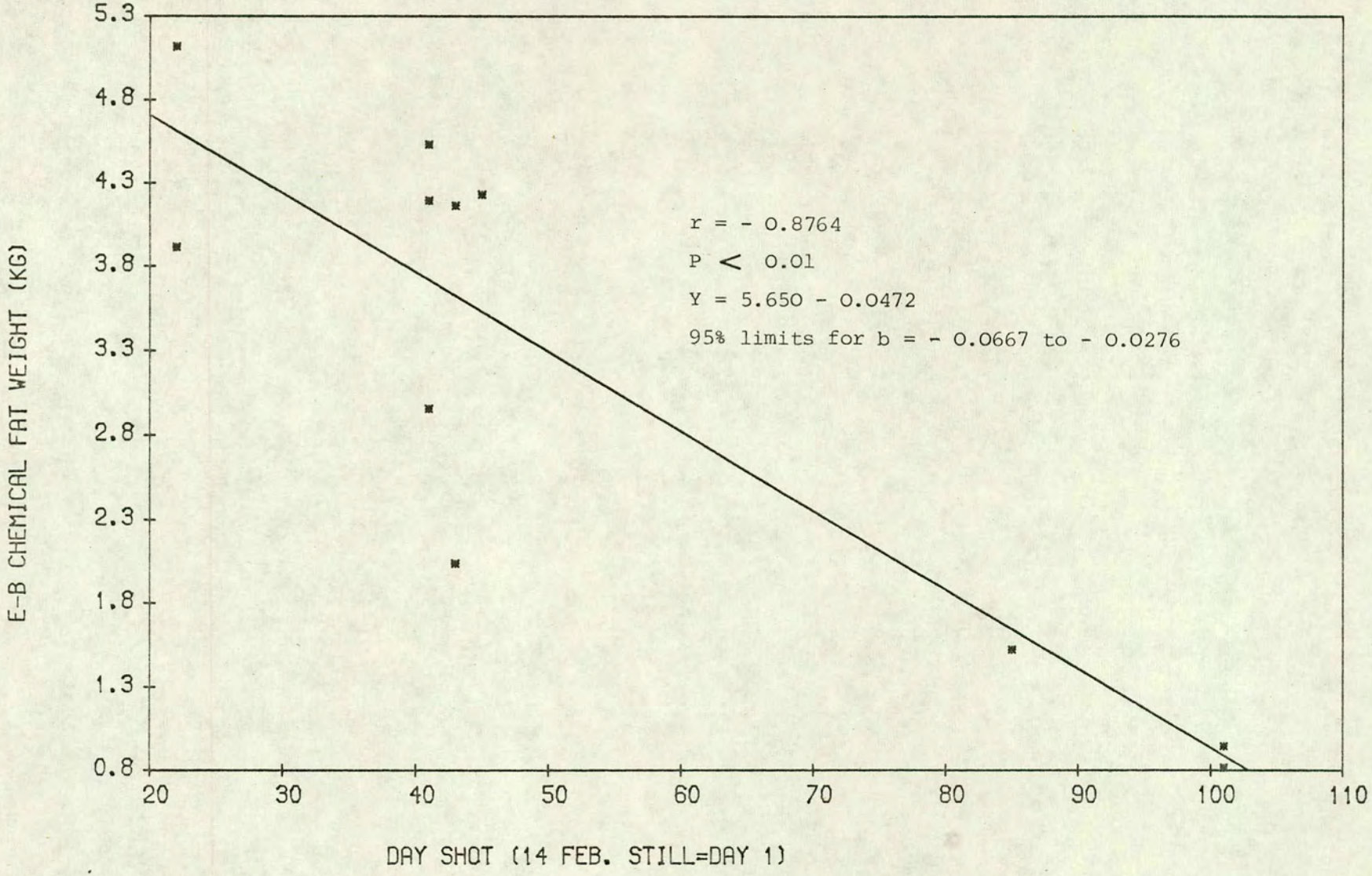


FIG. 5.6. E-B CHEMICAL FAT LOSS

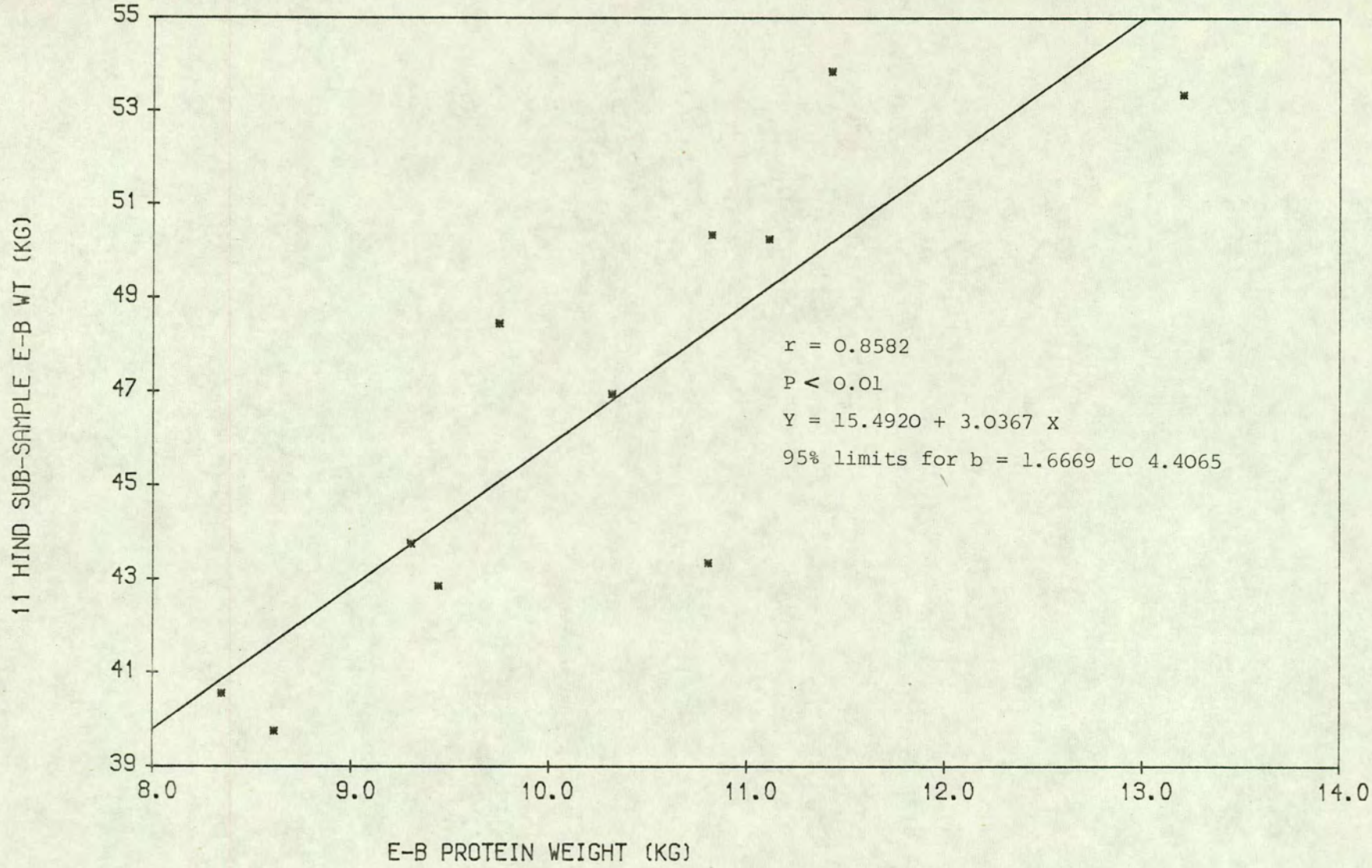


FIG. 5.7. E-B WT. RELATED TO PROTEIN WT.

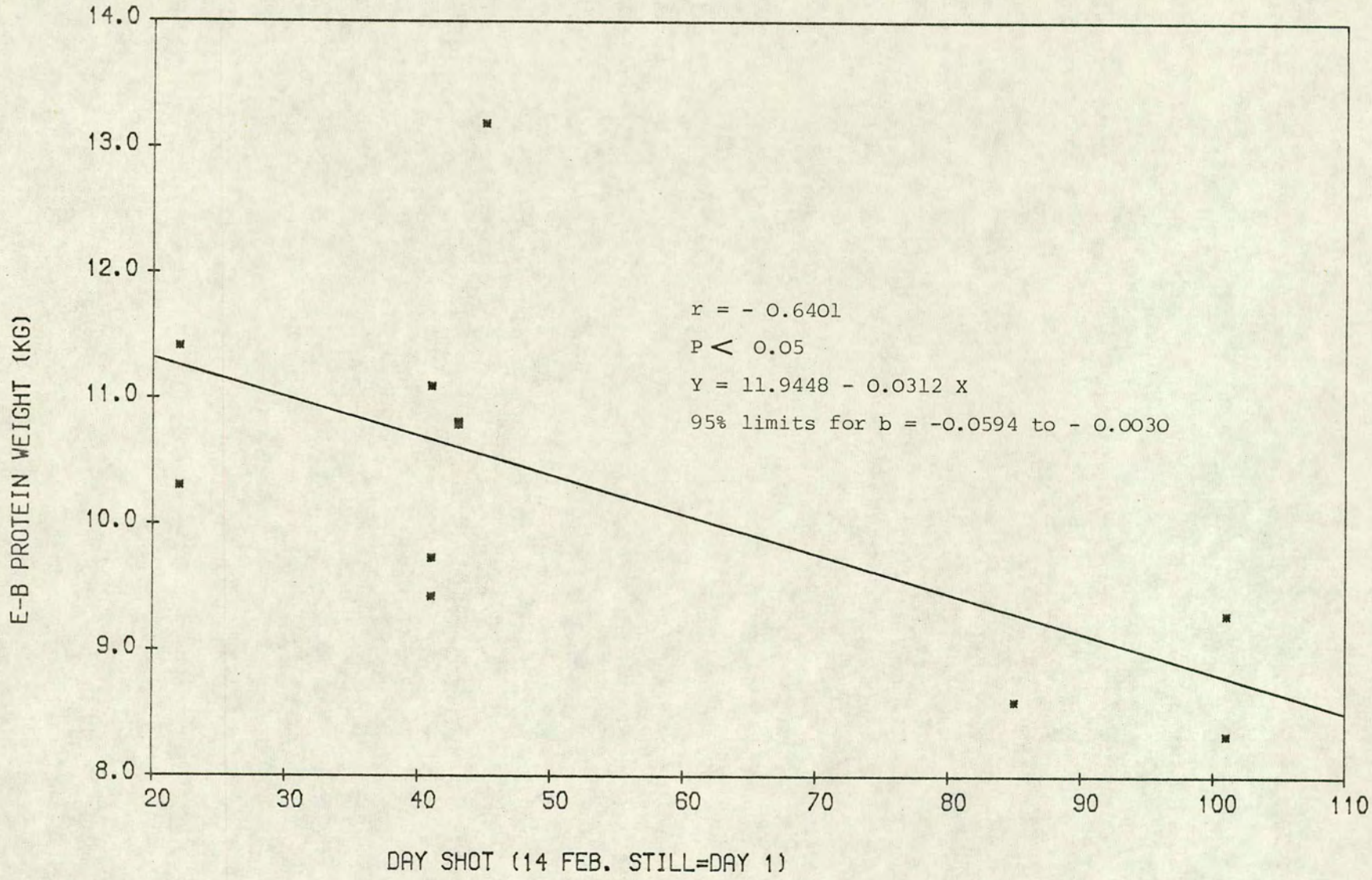


FIG. 5.8. E-B PROTEIN WEIGHT LOSS

the whole 100 days from 14 February to 25 May: $r = -0.648$, $P < 0.05$). If this be so, it is in agreement with the finding of Butterfield (1966), during a study of semi-starvation of young (19 month-old) beef cattle, that although the greatest relative tissue change occurred in dissectible fat, which lost 69.7% of its original weight, the actual weight loss of muscular tissue was 1.18 times greater than that of fatty tissue. There is no evidence from the present study to suggest any such drastic losses of dissectible muscular tissue: an estimated drop of around 0.640 kg of dissected muscle tissue occurred in the loin and ribs joints of the butcher's half carcass (0.26 kg and 0.38 kg, respectively) over the whole 100 days, compared to an estimated loss of around 8.9 kg of dissectible fatty tissue.

5.2. Empty body energy content and tissue composition.

In recent years a number of studies have been made of the energy content of the bodies of domestic ruminants, and methods of estimating energy content from empty-body weight have been variously derived from regression analysis. It is unfortunate that the published results of most of this research have not included data on the energy content of DM only, instead usually presenting values for the content of the whole empty body. Because of the uncertainty concerning the amount to which the DM contents of the representative samples (made of the empty bodies of the hinds in this research) are overestimates, caution must be exercised in comparing the amounts of energy and other components of their empty bodies with the results of studies of other ruminants. However, Ulyatt and Barton (1963), in a study of the statistical relationship between the chemical and

dissectible components of the empty bodies of sheep, found the average DM content of muscular tissue in their animals to be around 31 percent: in the present study the average DM content of the muscle of the six hinds analysed in detail was found to be 27.9 percent. The fact that the determined DM content varied so little (group 1 muscle DM content was 27.4; group 2, 28.1; group 3, 28.2; and group 4, 28.0), and furthermore the average is lower than that found by Ulyatt and Barton in sheep muscle, in spite of being a presumed overestimate, is taken to be an indication that once the hinds which had obviously undergone considerable moisture loss were removed (Figure 5.1), the error in the estimation of the DM content of the remaining sub-sample is small enough to allow comparisons to be made, with care, between the results of the analyses made upon them, and those of studies of the composition of other ruminants.

Some regression equations describing the relationship between empty-body weight and its energy content, and the weights of the major body components as determined in particular studies of cattle and sheep, and in this research for red deer, are shown in Table 5.2 overleaf.

Table 5.2: some simple linear relationships between chemically-determined components (Y) of the empty body and empty-body weight (X).

Item	Estimating equation	Correlation coefficient	R^2 value	Animal	Source
energy content (Mcal)	$Y = -30.68 + 4.135\ X$		0.966	Sheep	Burton & Reid (1969)
	$Y = -549.3 + 4.381\ X$		0.786	Cattle	Reid & Robb (1971)
	$Y = -2.534 + 1.650\ X$	0.99		White-tailed deer.	Robbins et al. (1974)
	$Y = -82.93 + 3.740\ X$	0.96	0.921	Red Deer.	Present Research
water content (kg)	$Y = 2.73 + 0.478\ X$		0.978	Sheep	
	$Y = 8.07 + 0.466\ X$	0.971	0.943	Red Deer.	
	$\log_e Y = -0.103 + 0.902 \log_e X$	0.999		White-tailed deer.	
	$\log_e Y = 0.609 + 0.725 \log_e X$	0.971		Red deer.	
protein content (kg)	$Y = 0.690 + 0.127\ X$		0.972	Sheep	
	$Y = 11.20 + 0.149\ X$		0.886	Cattle	
	$Y = -1.046 + 0.242\ X$	0.858	0.736	Red deer.	
	$\log_e Y = -1.602 + 1.0001 \log_e X$	0.998		White-tailed deer.	
	$\log_e Y = -1.866 + 1.0909 \log_e X$	0.868		Red deer.	
fat contents	$Y = -3.64 + 0.364\ X$		0.935	Sheep	
	$Y = -61.6 + 0.367\ X$		0.694	Cattle	
	$Y = -9.83 + 0.278\ X$	0.890	0.792	Red deer.	
	$\log_e Y = -5.836 + 1.999 \log_e X$	0.983		White-tailed deer.	
	$\log_e Y = -18.20 + 4.998 \log_e X$	0.813		Red deer.	

The relatively good ability of empty-body weight of the hinds to predict the empty-body gross energy content (as can be seen from the R^2 value in Table 5.2; see also Figure 5.9) is somewhat surprising, considering that the 11 sub-sample hinds were all adults. As Reid and Robb (1971) and others (e.g. Young and Corbett, 1972; Garret and Hinman, 1969) have pointed out, the relationship between energy content and body weight in adult animals is usually much more variable than is that in young animals (which the sheep of Burton and Reid, 1969, and the white-tailed deer of Robbins et al., 1974, were), because of the mobility of fat, protein and water in the tissues of older animals. The high correlation between estimated empty-body gross energy content and the empty-body weights of the sub-sample hinds seems to be yet further evidence of the importance of energy status in controlling the body weights of hinds. The energy content of body tissue weight gain or loss (the relative size of which is indicated by the size of the regression coefficients in the equations given in Table 5.2) has been found to be highly variable; values determined in cattle, for instance, having ranged from 4.8 to 9.4 Mcal/kg body weight gain, and from 6.3 to 7.9 Mcal/kg of body weight loss (Reid and Robb, 1971). This high variability reflects the differences in efficiency of utilisation of energy during synthesis or katabolism of fat or protein tissue, the differences that can occur in the tissues contributing to weight change, and the ability of water to mask the loss or gain of fat or protein weight. (Young and Corbett, 1972) have pointed out that even at constant body weight, energy content changes can be occurring).

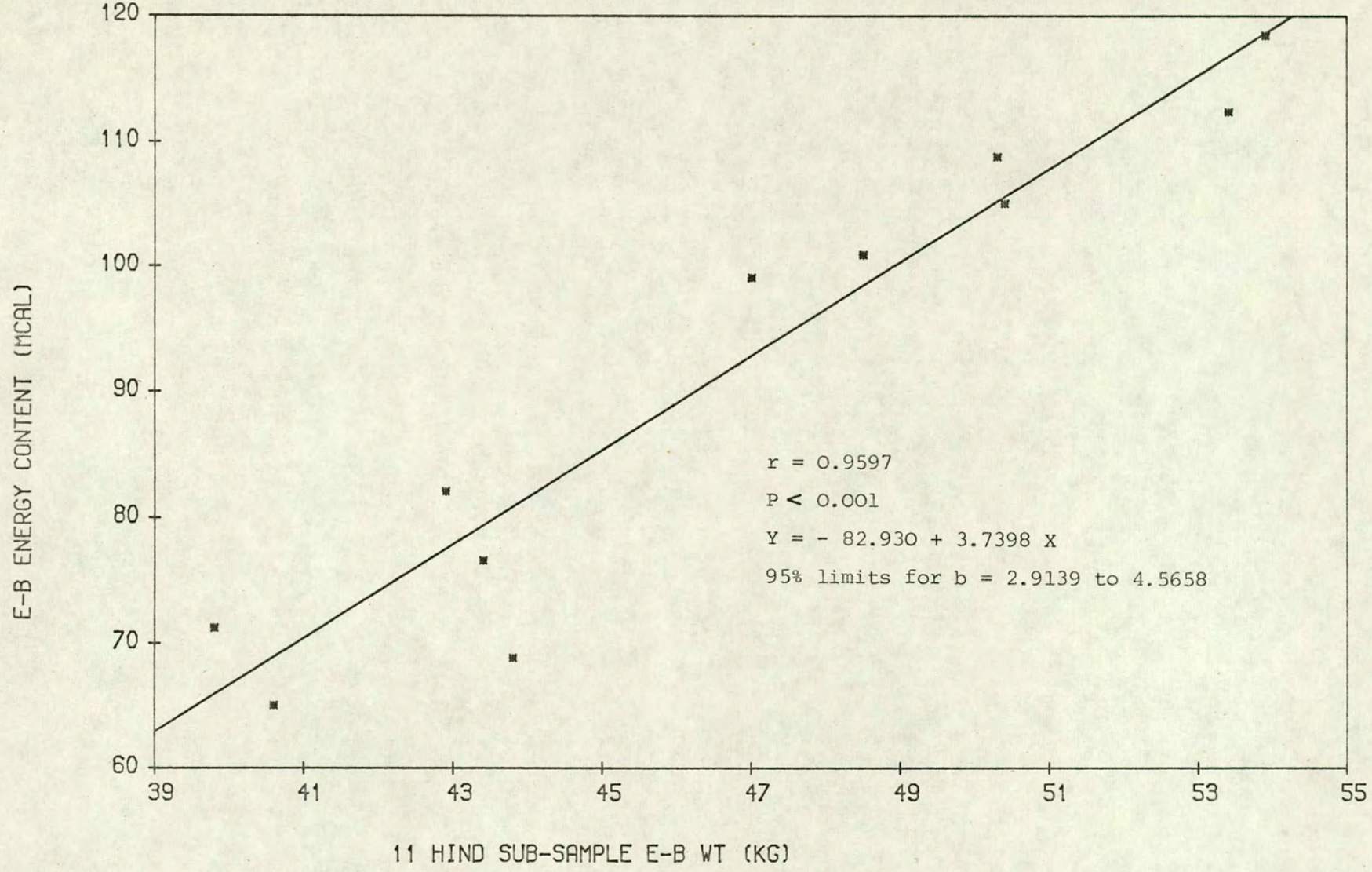


FIG. 5.9. ENERGY CONTENT RELATED TO E-B WT

The relatively small size of the regression coefficient in the equation derived by Robbins et al. (1974), describing the relationship between the empty-body weight of their white-tailed deer and gross energy content, presumably is an indication of the low fat content of the gains in weight which these young growing deer were undergoing. The relatively large size of the coefficient derived from the 11 sub-sample hinds is taken to be further evidence that the losses in body weight the hinds underwent were largely due to the loss of high-energy-content fat (see Figures 5.10 and 5.11). Thus the change in energy content per unit change in body weight is high, as indicated by the large regression coefficient. It should be emphasised, however, that the values derived from analysis of the data of either the 11 sub-sample or all 19 hinds are indications only of the changes occurring in pregnant adult hinds which are losing body weight. The calorific value per unit of body weight change can vary according to whether weight is being gained or lost, the relative proportions of the tissues involved, and, when weight is being gained, possibly even depending on the diet which gives rise to the gain.

That the weight loss suffered by the sub-sample hinds consisted largely of fat further is evidenced by comparison of the regression coefficients given in Table 5.2 describing the relationship between empty-body weight and fat weight. The slightly larger coefficient in the chemical fat weight equation is taken to be an indication that change in empty-body weight had a relatively greater effect on weight of fat (and vice versa) than it did on the weight of protein in the body (see also Figure 5.12).

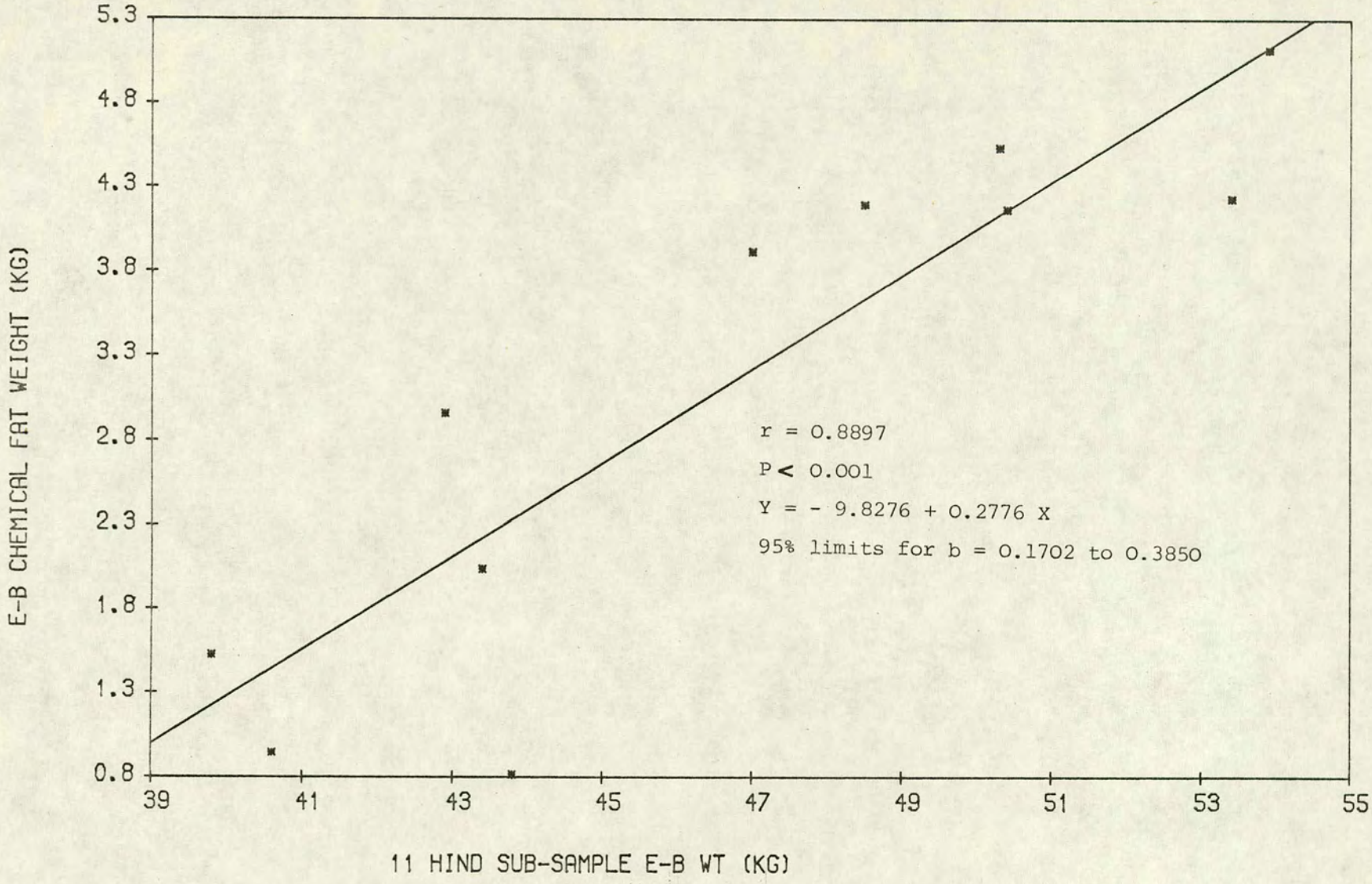


FIG.5.10. CHEMICAL FAT RELATED TO E-B WT.

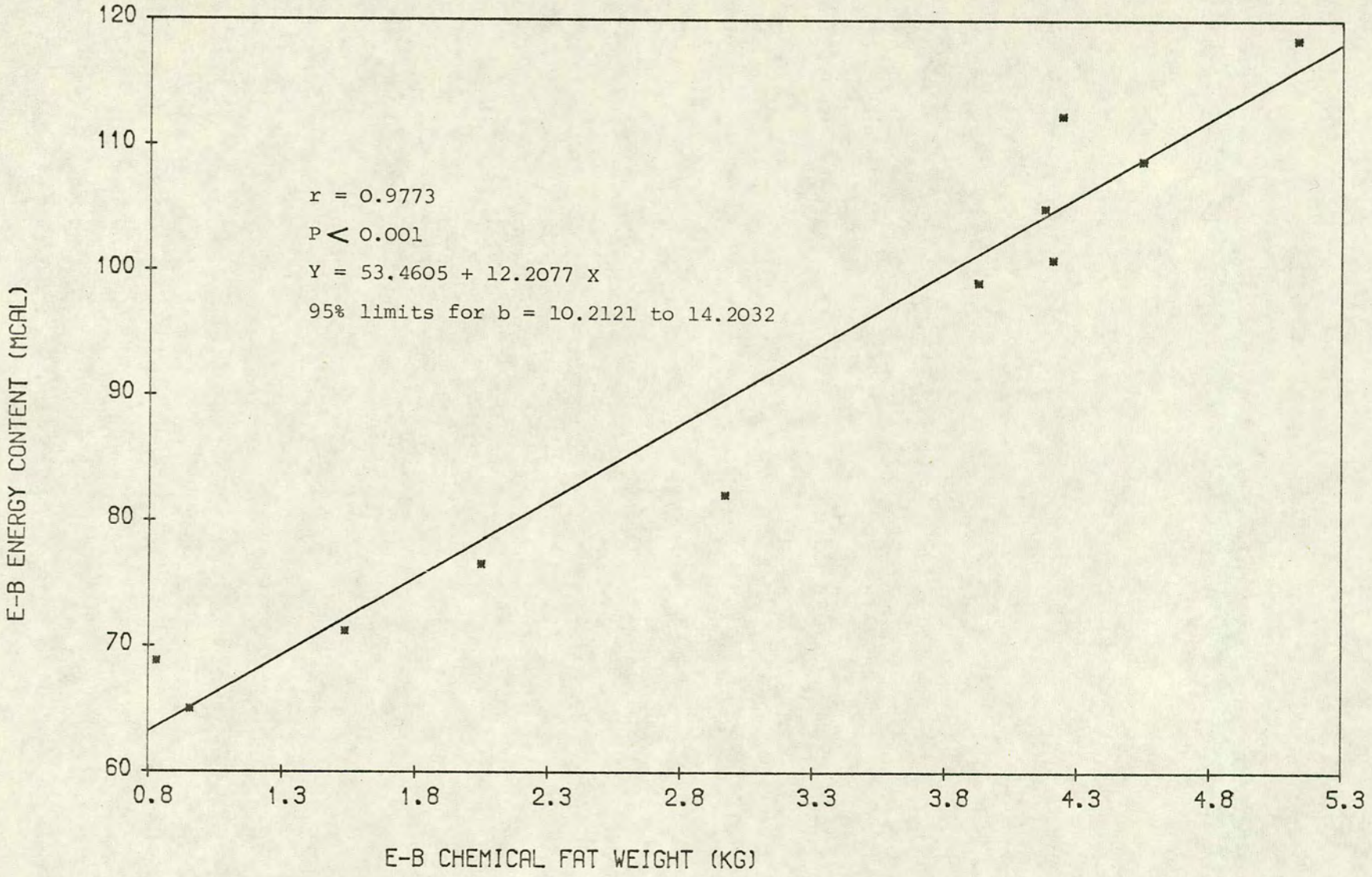


FIG.5.11. ENERGY CONTENT RELATED TO FAT WT.

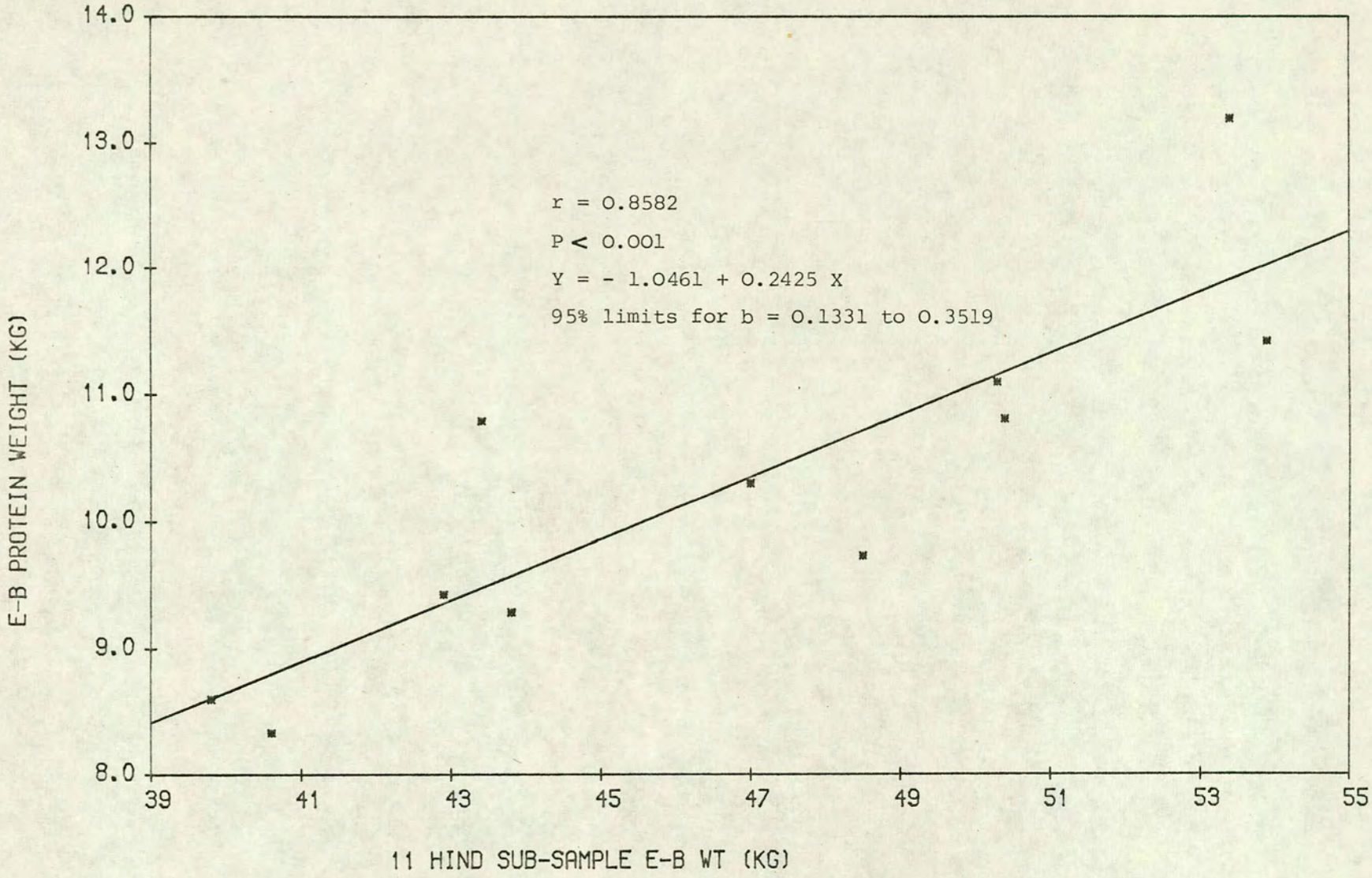


FIG.5.12.PROTEIN WT. RELATED TO E-B WT.

The considerably larger size of the regression coefficient in the equation describing fat and empty-body weight in red deer as compared to that for white-tailed deer, and the very similar sizes of the coefficients describing protein weight, are taken to be reflections of the differences in the animals and situations from which the equations were derived. The deer of Robbins et al. appear to resemble most young, growing animals, in that their weight gains consisted mostly of muscle and bone tissue, and relatively little fat, while the weight losses which the hinds of this study were undergoing consisted of a high proportion of fat.

The larger sizes of the regression coefficients describing the relationships between empty-body weight and protein weight in both red and white-tailed deer, as opposed to those describing cattle and sheep, presumably are a reflection of the fact that even 'fat' deer in good condition proportionally have less fat in their bodies than do most sheep or cattle. Thus hind 17 had only about 11% chemical fat in her empty-body weight, and only about 3% of the weight of her half carcass weight was contributed by dissectible fatty tissue compared to 25% fat in the empty bodies of beef steers (Garret and Hinman, 1969), 31% and more in the bodies of sheep (Burton and Reid, 1969), and 10.6% fat in the carcass weight of water buffalo (Bubalus bubalis; Charles and Johnson, 1972). The low fat content of the deer is in keeping with the comparisons made by Ledger (1963) between very fat steers, having a carcass weight which consisted of around 40% fat, with the majority of wild ruminants he looked at in East Africa, which had less than 5% fat in their carcass weights. However, because of the mobility of

body fat (as has been amply demonstrated in this and the previous two chapters in red deer), it is questionable to compare levels of fatness between species, or even between individuals, unless the beasts concerned are of similar age, and have been exposed to similar dietary and environmental regimes.

The similarity of the regression coefficients in the equations describing the relationships between empty-body weights and weights of water in the bodies of red deer, white-tailed deer and sheep appears to indicate the change in water content per unit of body weight change may be similar in the three species. Although the water loss during storage of the 11 sub-sample hinds means that the data describing their water contents can only be accepted as a rough indication of body water content, the considerably larger constant in the equation describing the relationship between empty-body weight and water weight in red deer; as compared to that for sheep, may be an indication that the water content of the bodies of red deer is rather higher in general than is that in the bodies of sheep. Since red deer appear to have proportionally more muscle tissue in their bodies, and much of the water content of the body is within muscle tissue, such a finding would not be surprising.

5.3. Proportional and chemical changes in body tissues and components.

Neither the percentages of muscle nor of bone in the weight of the half carcass of the 19 sample hinds showed any significant change individually over the 100-day studied period, but the weights of bone and muscle tissues together increased significantly in their percent contribution to half carcass weight over the period (from around 92% to around 96%).

This increase was accompanied by a corresponding decrease in the percentage of half carcass weight contributed by dissectible fat, from around 6% to around only 0.8%. The weight of the non-carcass (i.e. the offal, or head, pelt, feet and internal organs) component of empty-body weight rose from around 27% to around 33% over the 100 day period (see also Chapter 4; section 4.3).

5.3.1. CHANGES WITHIN THE MUSCLE, BONE AND FAT TISSUES OF THE HALF CARCASS.

Muscle tissue.

The high correlation found between the DM content of a tissue and the amount of fat present in that tissue (see Chapter 3, section 3.4) means that when DM content is observed to fall, a drop in fat content probably has also taken place. As can be seen in Table 5.3, the percentage of chemical fat in every tissue of the carcasses of the six hinds analysed in detail decreased over the 100 days from which they were collected. Because of the small sample size, some of the correlations between decrease in chemical fat percentage and time are not significant, but it is thought that in all such cases, the correlation would be found to be so in a larger sample. It can also be seen from the table that the DM content of nearly every tissue of the half carcass dropped, in most cases significantly. DM contents of the muscle tissues of the hind shank and group 4 appear to change only slightly over the mid-February to end of May period. The probable reason for this is that the amounts of fat contained in these tissues (group 4 consists of the haunch, loin and ribs joints) are small, relative to the weights of muscle present. For example, intramuscular fat (i.e. that contained within the muscle tissue

Table 5.3. Correlation coefficients between time and various chemical constituents of the tissues of the six hinds examined in detail. (A statistically significant correlation suggests that the particular constituent increases or decreases its contribution to overall composition, over the period mid-February to June.)

Constituent: in:	Dry matter	Ash	Nitrogen	Fat
Group 1				
muscle	r = - 0.30 (N.S.)	- 0.47 (N.S.)	+ 0.75 (P<0.1)	- 0.83 (P<0.05)
bone	r = - 0.88 (P<0.05)	+ 0.68 (N.S.)	+ 0.96 (P<0.005)	- 0.62 (N.S.)
fat	r = + 0.48 (N.S.)	(no determinations)		- 0.48 (N.S.)
Group 2				
muscle	r = + 0.12 (N.S.)	+ 0.39 (N.S.)	+ 0.62 (N.S.)	- 0.84 (P<0.05)
bone	r = - 0.92 (P<0.01)	+ 0.59 (N.S.)	+ 0.74 (P<0.5)	- 0.62 (N.S.)
fat	r = - 0.51 (N.S.)	(no determinations)		- 0.78 (P<0.1)
Group 3				
muscle	r = - 0.85 (P<0.05)	+ 0.76 (P<0.1)	+ 0.95 (P<0.05)	- 0.89 (P<0.02)
fat	r = - 0.91 (P<0.02)	+ 0.98 (P<0.05)	+ 0.99 (P<0.1)	- 0.96 (P<0.01)
Group 4				
muscle	r = + 0.36 (N.S.)	+ 0.76 (N.S.)	+ 0.76 (P<0.1)	- 0.85 (P<0.05)
bone	r = - 0.66 (N.S.)	+ 0.78 (P<0.1)	+ 0.68 (N.S.)	- 0.84 (P<0.05)
fat	r = - 0.87 (P<0.1)	+ 0.89 (P<0.05)	+ 0.85 (P<0.1)	- 0.86 (P<0.1)

itself) in hind 17's haunch shank contributed only 2% to the weight of the dissectible muscle, and was only around 7% of the weight of DM present (see also Chapter 3, Table 3.3). No evidence was found of change in the DM content of the muscle of the fore shank; this tissue also has very little fat in it.

Although the DM content of the fore shank did not appear to change, and decreased only slightly in the muscle of the haunch, loin and ribs, that of the shoulder and neck muscle tissue (group 3) significantly decreased. Presumably this occurred because of the relatively high (16% in hind 17) initial level of intramuscular fat in this tissue. It is a pity that I minced together and analysed the tissues of the upper haunch, loin and ribs joints as a single group, since it appears that the changes which occur within these areas of the carcass differ: decreases seem to be occurring in all three (muscle, bone and fatty) tissues of the loin and the ribs, but only in the intermuscular (i.e. associated) fatty tissue of the haunch. Since the haunch is by far the largest single component of this group, contributing much more to half carcass total weight than do the loin or the ribs (22% as compared to a collective 12% in hind 17, and 26% as compared to only 9.5% in hind 35), the changes suspected to be occurring in the chemical composition of the latter two areas will have been masked by the apparent stability of the tissues composition of the haunch.

The ash content of the muscular tissue decreased slightly in the haunch shanks of the six sub-sampled-chemically hinds, but increased in the muscle of the other areas of the carcass (although only that in the shoulder and neck muscle

was significant). Presumably this is a reflection of the decrease occurring in the intramuscular fat of this area.

The percentage of nitrogen increased in all the muscle tissues of the half carcass (see Table 5.3; that in group 2, fore shank, probably would have been found significant in a larger sample), the increase being only very slight (from around 13 to 14%). There was virtually no correlation found between time and the weights of protein in the individual joints; except the shoulder, where protein weight appeared to decrease ($r = -0.52$, $P < 01$). Yet the weight of protein in the whole empty body appears to have decreased significantly: combining the suggestion of a possible drop in protein in the shoulder and neck with the evidence of a decrease in the percentage of the half carcass muscle weight located in the other 'trunk' areas of the carcass (i.e. the loin and the ribs) suggests that some of the protein loss may be occurring from within these three joints.

The intramuscular fat of the half carcass virtually completely disappeared over the studied period mid-February to the end of May. The drop in the hind and fore shank musculature was from around 7%, and in the shoulder, neck, haunch, loin and ribs from around 14%, to less than 1% of the weight of muscle in all areas of the carcass.

Bone tissue.

The DM content of bone tissue was found to drop over the 100 day period in all three areas of the half carcass in which it was determined (Table 5.3). The drop observed in the bone of group 4 was not significant, but the rather high correlation coefficient ($r = -0.66$) suggests that with

a larger sample it would have been. This decrease probably occurs because of the loss of chemical fat from the marrow of the bone tissues. However, the drops in the DM content of both the fore (tibia and fibula) and hind (radius and ulna) shank bones appear slightly too high to be explained simply by the loss of marrow fat. Whether this is due to sampling error, or reflects possibly a loss of some minerals through mobilisation is not known, but it seems unlikely, because of the obvious importance of these bones to such a mobile animal as the red deer, that mineral mobilisation would occur within them. Much more likely, and in keeping with the suggestion that the weights of bone in the loin and ribs are decreasing in relation to the rest of the half carcass bone over the studied period, is that if mobilisation must occur, it does so within the bones of these areas of the body.

As in muscle tissue, the increases found in the percentage of ash in bone tissue appear to be due to the disappearance of chemical fat. Thus the percentage of ash in the DM of the group 1 (hind shank) bone rose by around 6.5% over the 100 days, while fat content dropped by around 10% in the DM: in group 2 bone, ash increased by about 12% while fat dropped by around 11%: in group 4 bone the percentage of ash in the DM rose by around 10%. while that of fat fell by around 17%.

The nitrogen content of all bone tissue was found to increase slightly (by around 2%) over the studied period. The explanation for this would seem to be because of the disappearance of fat from the bone marrow.

Intermuscular (associated) fatty tissue.

The DM content of dissected intermuscular tissue dropped in all areas of the half carcass but group 1 (the hind shank). Unfortunately ash and nitrogen contents were only determined for the intermuscular fatty tissues of groups 3 and 4; the contents in the DM of both ash and nitrogen increased in both of these areas.

The actual fat content of all carcass dissectible fatty tissue dropped considerably over the 100 day period. The correlation between time and the percentage of fat in the DM of the fatty tissue of group 1 was not significant ($r = -0.48$, $P > 0.1$), but I think that with a larger sample it would have been. The derived regression equation estimated that the percent fat in the fatty tissue of group 1 fell from around 57% to only around 26% over the studied period. The percent fat in the DM of the intermuscular tissue of group 2 (the fore shank) dropped significantly; the decrease is estimated by the regression equation to have been from around 76% to only around 25%. The drop in group 3 tissue is estimated to have been from around 90% fat to around only 20%. The drop in group 4 is estimated to have been from around 94% to around only 33%.

5.3.2. CHANGES IN THE NON-CARCASS COMPONENTS OF THE BODY.

As discussed in section 4.2 of Chapter 4, the increase in the percentage of the empty-body weight contributed by the head is probably an indication that the head loses little weight over the studied period. The increase is similar to the finding by Gunn (1965) that the heads of sheep experimentally raised on a diet low in energy increased in their contribution to body weight, to become proportionally heavier than were those of sheep raised on a high nutritional plane.

However, some fat is contained in the marrow cavity of the mandibular bones, and determination of the levels of fat present in the mandibular cavities has been proposed as an indicator of condition in white-tailed deer (Baker and Leuth, 1966; Nichols and Pelton, 1973). Nichols and Pelton found that the fat content of the cavity tissue decreased from around 84% in white-tailed deer killed in Tennessee in the winter period of late December, to around 78.9% in early January. The DM, ash, nitrogen and fat contents of the whole mandibles of four hinds collected during this present study were determined (hinds 17, 30, 32 and 35). None of the constituents determined were found to change significantly, statistically, over the period they were collected, but the high correlations with time (shown in Table 5.3) suggest that they would have been found to do so had a larger sample been available. The DM content of the whole mandibles decreased from 76% in hind 17 to 66% in hind 35 ($r = -0.564$, $P > 0.1$). The percentage of fat in the DM decreased from 9% to only 3.5% ($r = -0.90$), but because of the small sample size this cannot be shown to be significant. The regression derived from this data estimated that a pair of mandibles weighing, for instance, 300g, would contain around 21g of fat in the marrow cavity, and that this would have fallen to only around 7g by the end of May.

The increase in the percentage of empty-body weight contributed by the empty gut in the 19 sampled hinds may be an indication that the intestinal tract of red deer increases somewhat in weight and possibly therefore length during periods of poor herbage quality. Such an adaptation has been found in a variety of wild ruminants in East Africa

(Ledger, 1968), and Gunn (1965) found that sheep raised on restricted diets of high fibre content developed heavier digestive systems than did ewes raised on higher quality diets.

Whether or not the stomach, heart, liver or kidneys were undergoing weight losses in the collected hinds cannot be ascertained from the available data (because of the differences in age and initial size of the sampled hinds). However, Mitchell et al. (1976) have shown that the liver and kidneys of Scottish red deer undergo cyclic changes in weight over the year, and that both organs are decreasing in weight during the period from which the sampled hinds were taken.

5.3.3. DIFFERENTIAL RATES OF WEIGHT LOSS BETWEEN BODY AREAS.

The changes found occurring within the tissues of the half carcass of the 19 sampled hinds are similar to those found in cattle and sheep which have been subject to periods of undernutrition, and basically are opposite in occurrence and effect to the changes in domestic animals which are putting on weight. Thedifferential effects of undernutrition on the tissues in the different areas of the half carcass of all 19 hinds in general are in keeping with the theory that late developing tissues are most affected by varying levels of nutrition (either in gaining or losing weight), while the earlier developing tissues are least so. Thus the hinds sampled in this study appear to have been losing weight particularly from the areas of the loin and the ribs, to a lesser extent from the shoulder and neck, an even lesser extent from the haunch, and virtually not at all from the fore and hind shanks. Studies of the body

composition of sheep (e.g. Panaretto, 1964; Gunn, 1965; Field et al., 1968; Sykes et al., 1974) and of cattle (e.g. Butterfield, 1966) which had been losing weight at the time of slaughter and examination, have found similar differences in the location and extent of tissue weight losses.

Changes occurring in the tissues of growing ruminants appear to occur in the reverse order to that in which tissues are depleted during periods of undernutrition. Thus Murray et al. (1974), in a study of growing cattle, found that the percentages of the muscle and of bone weights in the half carcass decreased as carcass weight increased; whereas the percentages of muscle and of bone in the half carcasses of the hinds of this study increased as carcass weight dropped. Murray et al. also found that the cervical vertebrae of their growing cattle increased in weight at a rate greater than that of total carcass bone, while the equivalent bones (loin joint bone) decreased in the red deer of this study. Butterfield (1966) summed up the apparently general process of tissue depletion during periods of undernutrition when he stated (in reference to muscular tissue loss in cattle); "The practical implications of these changes within the musculature are of particular interest. Those muscles which are most required by the under-fed animal in its search for further food have a high priority for available nutrients so that in older animals, when semi-starved, the highest priority for the limited nutrition of the musculature is enjoyed by the limb muscles most likely to aid in the survival of the animal." The results of the present study on red deer show that not only are the muscles that are most used in the search for food given the highest nutrient prior-

ity (thus losing least weight), but so also are their related bones, and, perhaps surprisingly, apparently their associated fatty tissues to a certain extent as well.

5.4. Changes in mineral content.

Interpreting the results of the determinations of the mineral contents of the 19 sampled hinds, in terms of their possible importance to productive performance by red deer, is difficult, in view of the lack of a suitable basic standard with which to compare the levels of the major mineral nutrients as found. As reported in section 3.1.5. of Chapter 3, the only statistically significant changes found in the concentrations of the major mineral nutrients, in the DM of the 100g representativessamples of the 19 hinds, was the minute increase in the percentage of magnesium present (from around 0.133% to around 0.137% of the DM). The average concentration of magnesium in the bodies of the 19 hinds was 0.056% of the empty-body weight, as compared to the usual average amongst domestic ruminants of around 0.04% (MacDonald et al., 1973): however, the hind sample is too small for this to be taken as proof that the concentration of magnesium in red deer hinds is higher than it is in most other animals.

Why the percentage of magnesium in the empty bodies of the sampled hinds should have significantly increased is not immediately obvious. The distribution of magnesium in the body tissues differs somewhat from that of calcium and phosphorus, in that the 'soft' (i.e. muscle, fat, nervous, etc.) tissues contain appreciable amounts of magnesium by comparison: only about 70% of total body magnesium is located in the skeleton, compared to around 99% of calcium, and

around 75 to 80% of phosphorus (A.R.C., 1965). However, like calcium and phosphorus, the majority of the magnesium content of the body is located within the skeleton, as compared to sodium or potassium, which are contained mostly within the soft tissues. These differences in location within the tissues of the body may explain the relationships found between these nutrients and the energy content of the 100g representative samples of the empty bodies of the 19 sampled hinds (see Table 5.4). It can be seen from the table that although the percentages of the major nutrients in the DM contents of the samples appear to increase over the studied period, only those of the minerals located mostly in bone (calcium, phosphorus and magnesium) do so significantly. Since the gross energy of the samples (and of the hinds) has been shown to be decreasing over the studied period, the correlations shown in Table 5.4 indicate that the levels of the minerals contained mainly in bone, proportionally rise over the winter and spring period. The dynamics of the nutrients located almost exclusively in the soft tissues of the body (sodium and potassium) cannot be commented on on the basis of the correlations shown in the table, but the actual weights of both of these nutrients in the representative samples were found to have dropped significantly over the studied period ($r = -0.616$, $P < 0.05$; and $r = -0.564$, $P < 0.02$, respectively). The apparently most likely explanation of these findings is that the amounts of sodium and potassium in red deer are decreasing over the winter/spring period, but that they are doing so at rates similar to that of DM content (so that their percentages in it do not change), and at rates slower than that with which energy is being lost from the representative

Table 5.4. Correlation matrix between the 100 g samples' gross energy content (kcal/g D.M.), time, and the percentages of the major mineral nutrients in sample D.M.

% CALCIUM IN 100 G SAMPLES	------					
	-0.662					
	0.000%					
	43.9%					
% PHOSPHORUS IN 100 G SAMPLS	+	++++++				
	-0.454	0.721				
	5.000%	0.040%				
	20.6%	52.0%				
% MAGNESIUM IN100G SAMPLES	------	++++++	++++++			
	-0.791	0.882	0.647			
	0.005%	0.001%	0.000%			
	62.5%	77.8%	41.9%			
% SODIUM IN 100G SAMPLES	.	+	.	.		
	-0.281	0.501	0.142	0.398		
	20.000%	3.000%	60.000%	9.000%		
	7.9%	25.1%	2.0%	15.8%		
% POTASSIUM IN 100G SAMPLES	.	.	.	.	.	
	-0.184	-0.083	-0.077	0.006	0.308	
	50.000%	70.000%	80.000%	98.000%	20.000%	
	3.4%	0.7%	0.6%	0.0%	9.5%	
TIME (14 FEB=DAY 1)	------	.	.	++	.	
	-0.806	0.255	0.344	0.531	-0.156	
	0.003%	30.000%	10.000%	2.000%	50.000%	
	64.9%	6.5%	11.9%	28.2%	2.4%	

SAMPLE ENERGY (KCAL/GDM)	% CALCIUM IN 100 G SAMPLES	% PHOSPHORUS IN 100 G SAMPLS	% MAGNESIUM IN100G SAMPLES	% SODIUM IN 100G SAMPLES

TIME (14 FEB=DAY 1)	.
	0.067
	80.000%
	0.5%

% POTASSIUM IN 100G SAMPLES

35 GO :

samples (so that they are negatively but non-significantly correlated with it). Indeed, since there is a strong indication that muscle (or at least some protein-containing tissue) is being katabolised and thus lost over the studied period, a fall in the levels of the minerals contained largely within such tissue is to be expected.

Although the data are far too few to be in any way conclusive, a possible insight into some of the characteristics of extreme dietary energy deficiency in red deer may be gleaned from inspection of the mineral status of certain individual hinds (see Table 3.2). Throughout the analysis and inspection of the data from the 19 sampled hinds, particular hinds have been observed to differ in various aspects from the remainder of the sample population. These hinds are numbers 20, 30, and in particular, hind 23. Although the data describing other hinds may be further from the norm with reference to any single aspect, the combined evidence of tissue (especially fat) percentage distribution, and composition, energy contents, foetal weights (see Chapter 6) and mineral levels point to these hinds as being in relatively poorer condition at the times when they were shot than were the other beasts shot on or near the same dates. Thus the DM of the samples representing hinds 20 and 23 are both particularly high in sodium and potassium, and that of hinds 23 and 30 are noticeably higher in calcium and magnesium. This presumably is a reflection that these hinds were abnormally poor in condition for the particular times of season, containing relatively less fat, and therefore consisting more of only muscle and bone. However, hind 23 had an abnormally high sodium content while the other two did not; hind 30 had an abnormally high potas-

sium content while the other two did not; and hinds 23 and 30 were particularly high in calcium content (in relation to the percentage in the DM of other beasts), while hind 20 was not. It therefore appears that hinds do not all necessarily respond to severe undernutrition in exactly the same manner, in terms of abnormal levels of particular mineral nutrients.

In the absence of any suitable control animals with which to compare nutrient levels, it is not possible to deduce from the data available from the sampled hinds whether they were suffering from a deficiency of any of the major mineral nutrients. (An attempt was made to obtain hinds from a semi-domesticated herd in a deer park in the Lowlands of Scotland, which could be analysed and designated as standards against which the mineral levels of wild hinds could be gauged, but for a variety of reasons this did not prove possible). The weights of the major nutrients in the empty bodies of the 19 sampled hinds (as estimated from percentage in the DM of the representative samples), expressed in terms of units of metabolic sizes (i.e., per kg of empty-body weight to the power 0.75) all appeared to decrease over the 100 days of the studied period, but only sodium ($r = -0.632$, $P < 0.005$) and potassium ($r = -0.712$, $P < 0.001$) did so significantly. It is not possible to decide whether the decreases in these two nutrients occurred because of dietary deficiency, or are simply reflections of the loss of soft tissues in which they are contained: certainly, a decrease in the weights of sodium and potassium present can be expected, simply due to the latter explanation.

5.5. Location of body fat depots and sequence of mobilisation.

As has been emphasised previously, reserves of body fat

can be vital to animals that are exposed to prolonged periods of dietary energy insufficiency. The results presented in the last two chapters of this thesis demonstrate that wild Scottish red deer are in just such a situation over much or all of late winter and early spring. Since the consequence of being unable to provide energy to the body when it is required may well be fatal, while available but limited energy may result in poor productive performance, a close examination of the body fat depots of red deer, and their sequence of mobilisation, is of obvious value.

The analysis of the chemical fat content carried out on the dissectible fatty tissues of the six hinds which were analysed in detail, demonstrates that the actual amount of chemical fat, available to the body on katabolism as an energy source, is not well indicated, during late winter and spring, by the weights of dissectible fatty tissue which may be present in the bodies of red deer hinds. By May both the DM of dissectible fatty tissue, and the percentage of chemical fat in the DM, were found to be very low compared to the DM and fat content of the same tissue in February. For example, the intermuscular (muscle associated) fatty tissue of the haunch, loin and ribs (group 4 joints) of the hind collected in February (hind 17) was 72% DM, of which 81% was chemical fat. In contrast, in the last hind collected (hind 35, on the 25th May), the DM of this fatty tissue was only 38%, and only 13% of this DM was chemical fat. Thus not only does dissectible fatty tissue greatly decrease over the period February to June, but the actual quantity of fat contained in it in the latter part of this period is considerably lower than is indicated by the weight of the dissectible tissue. For example, in mid-February a

hind may have, say, 200g of intermuscular fatty tissue in her haunch, loin and ribs, which contains in fact around 175g of chemical fat. By the end of May the weight of dissectible tissue would have decreased considerably, but simply to demonstrate the point, let us assume that 300g of dissectible fat is still present: the weight of chemical fat in this tissue, as indicated by the determinations on the six hinds given above, would be around 15 grammes.

The extreme variability of the relationship between dissectible fat and the amount of chemical fat it contains is in contrast to the variability between the two which Ulyatt and Barton (1963) established from a study of the relationship between the dissectible and chemical components of the tissues of sheep. Ulyatt and Barton found that the correlation between the weights of dissectible and chemical fat in the carcasses of the sheep they examined was 0.99, and that the dissectible fat could be well estimated by a derived regression equation (in which chemical fat was the independent variable). The usefulness of such an equation is questionable firstly because the normal situation surely is to know the weight of dissectible fat, and wish to estimate chemical fat from it (without having to expend the time and money to carry out chemical determinations). In any case, in the present study it was found that the weight of chemical fat present in a joint of the red deer carcass could not be estimated accurately by the weight of dissectible fatty tissue present (see Table 5.5). The reasons for this appear to be not only the variability in the amount of chemical fat contained in a unit weight of dissectible fat, but also because the amounts of chemical fat located intramuscularly, and in bone, within a particular joint or area of the carcass,

Table 5.5. Regression equations in which weight of dissectible fat (Y) is predicted from determined weight of chemical fat (X), derived from data on red deer (present study) and sheep (Ulyatt and Barton, 1963).

species	predicting equation	correlation coefficient	significance level
red deer	$Y = 3.276 + 0.426\ X$ [1]	0.688	50 %
red deer	$Y = 33.459 + 0.511\ X$ [2]	0.760	10 %
sheep	$Y = 1.06\ X + 0.12$ [3]	0.99	?

1) Equation derived from data on fat content of Group 2 fatty tissue.
2) Equation derived from data on fat content of Group 4 fatty tissue.
3) Equation derived from data on fat content of the loin of sheep.

Table 5.6.(b). The weights (as chemically determined) of fat located in various fat and other tissues in the half carcasses and offal portions of the six hinds analysed in detail.

HIND	INTRAMUSCULAR FAT (g)	INTERMUSCULAR FAT (g)	SUB-CUTANEOUS FAT (g)	KIDNEYS FAT (g)
17	460.5	446.4	350.7	272.5
20	141.2	40.4	0.0	0.0
24	214.5	74.1	3.4	0.0
30	115.6	77.6	0.0	0.0
32	129.1	56.1	0.0	7.1
35	12.0	7.2	4.0	1.6

HIND	BONE MARROW FAT (g)	OFFAL TISSUES FAT (g)	ESTIMATED TOTAL CARCASS FAT (g) [1]	ESTIMATED TOTAL E-B FAT (g) [2]	OFFAL (%) [3]
17	258.0	1897.0	3304.0	5201.2	36.5
20	280.4	197.0	924.0	1121.0	18.0
24	220.0	972.0	1024.1	1995.9	48.7
30	84.9	772.8	556.2	1329.0	58.2
32	152.5	803.1	682.5	1485.6	54.1
35	19.0	325.3	85.6	410.9	79.2

(1) = 1/2 carcass x's 2. (2) =(1) + offal (3) % total E-B fat

HIND NUMBER	GP1 INTRAMUSCULAR FAT (G)	GP2 INTRAMUSCULAR FAT (G)	GP3 INTRAMUSCULAR FAT (G)	GP4 INTRAMUSCULAR FAT (G)
17.0000	6.8924	11.5376	188.1325	253.9228
20.0000	4.1895	7.0546	76.2216	53.7425
24.0000	2.2803	8.0439	61.2772	142.9460
30.0000	1.6197	1.2893	67.3911	45.3460
32.0000	2.7941	5.6271	39.5968	81.1164
35.0000	0.6708	0.6219	0.8712	9.8296

GP1 BONE MARROW FAT (G)
36.3898
43.8190
46.2822
11.6216
34.7940
4.3189

22 GO :

GP2 BONE MARROW FAT (G)	GP4 BONE MARROWFAT (G)	GP1 INTERMUSCULAR FAT (G)	GP2 INTERMUSCULAR FAT (G)	GP3 INTERMUSCULAR FAT (G)
33.3962	162.2162	4.9305	13.9982	162.3692
31.2978	205.2341	11.1046	2.7042	26.5428
37.0518	136.6442	0.0000	6.9815	42.6100
7.3915	65.8524	19.3374	4.3785	30.8546
27.6517	90.0559	6.8835	3.7987	10.7184
4.5531	10.0516	0.5242	0.0000	0.3335

23 GO :

GP4 INTERMUSCULAR FAT (G)	GP1 SUB-CUTANEOUS FAT (G)	GP2 SUB-CUTANEOUS FAT (G)	GP3 SUB-CUTANEOUS FAT (G)	GP4 SUB-CUTANEOUS FAT (G)
265.1226	0.0000	0.0000	11.8600	338.8196
0.0000	0.0000	0.0000	0.0000	0.0000
24.4757	0.0000	0.0000	0.0000	3.3810
23.0152	0.0000	0.0000	0.0000	0.0000
34.7476	0.0000	0.0000	0.0000	0.0000
6.3129	0.0000	0.0000	0.0000	3.9415

24 GO :

Table 5.6.(a). Location of chemical fat in the various tissues (eg. intra- and intermuscular, sub-cutaneous, perirenal, etc) of the four groups of the half carcass.

can be quite variable (see Figure 5.13).

Because, as explained above, an estimation of the amount of chemical fat present in the carcasses of red deer, and available to them as an energy source, could be considerably overestimated by the weight of dissectible fatty tissue present, the following discussion of body fat depots is based only on the data from the six hinds that were analysed in detail (and so in which the chemical fat content of muscle, bone and fatty tissues are known). The weights of chemical fat located in the various depots of the body, and how these changed over the studied period, are given in Table 5.6 and shown in Figure 5.13.

The sub-sample of only six hinds is far too small to allow one to accept with confidence that regression equations derived from it to describe the changes occurring within the body fat depots, accurately describe the rates at which fat in the various locations is depleted from the bodies of the majority of wild hinds over the studied period. However, in the absence of other data, these regressions are presented, in the hope that they at least give not grossly inaccurate indications of the relative distribution of fat throughout the carcass and the body, and how this distribution may change as the winter/spring period of dietary energy insufficiency progresses.

From the data on the six hinds analysed in detail the distribution of fat in the body around the middle of February appears to resemble the following:

fat located in the non-carcass (offal): 36%
fat in the carcass (total half-carcass X's 2) 64%

Thus the minority of the fat appears to be located at this period in the offal (e.g. mesenteric, and organ-associated

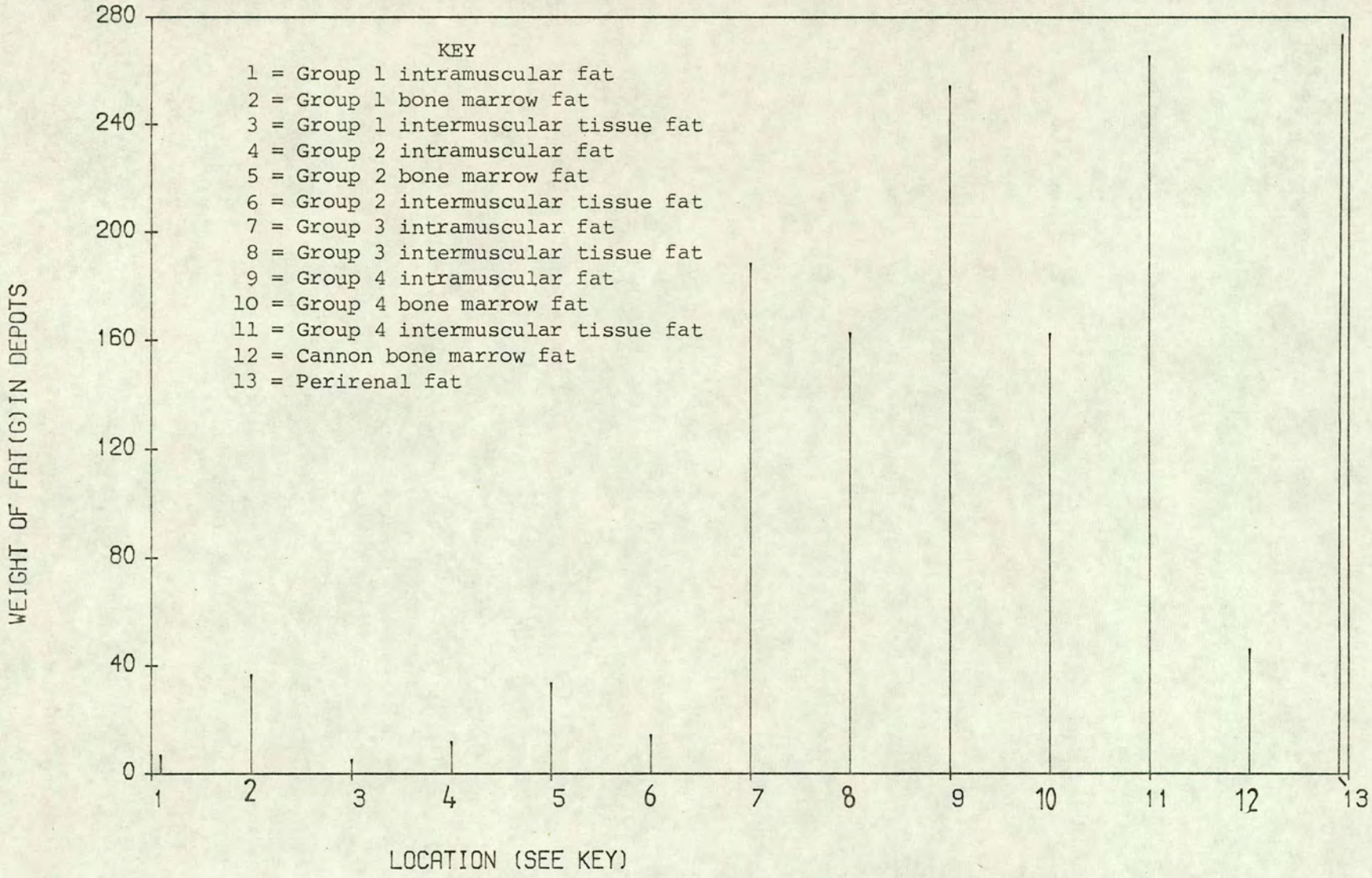


FIG.5.13.A FAT DEPOTS IN 1/2 CARCASS OF HIND 17.

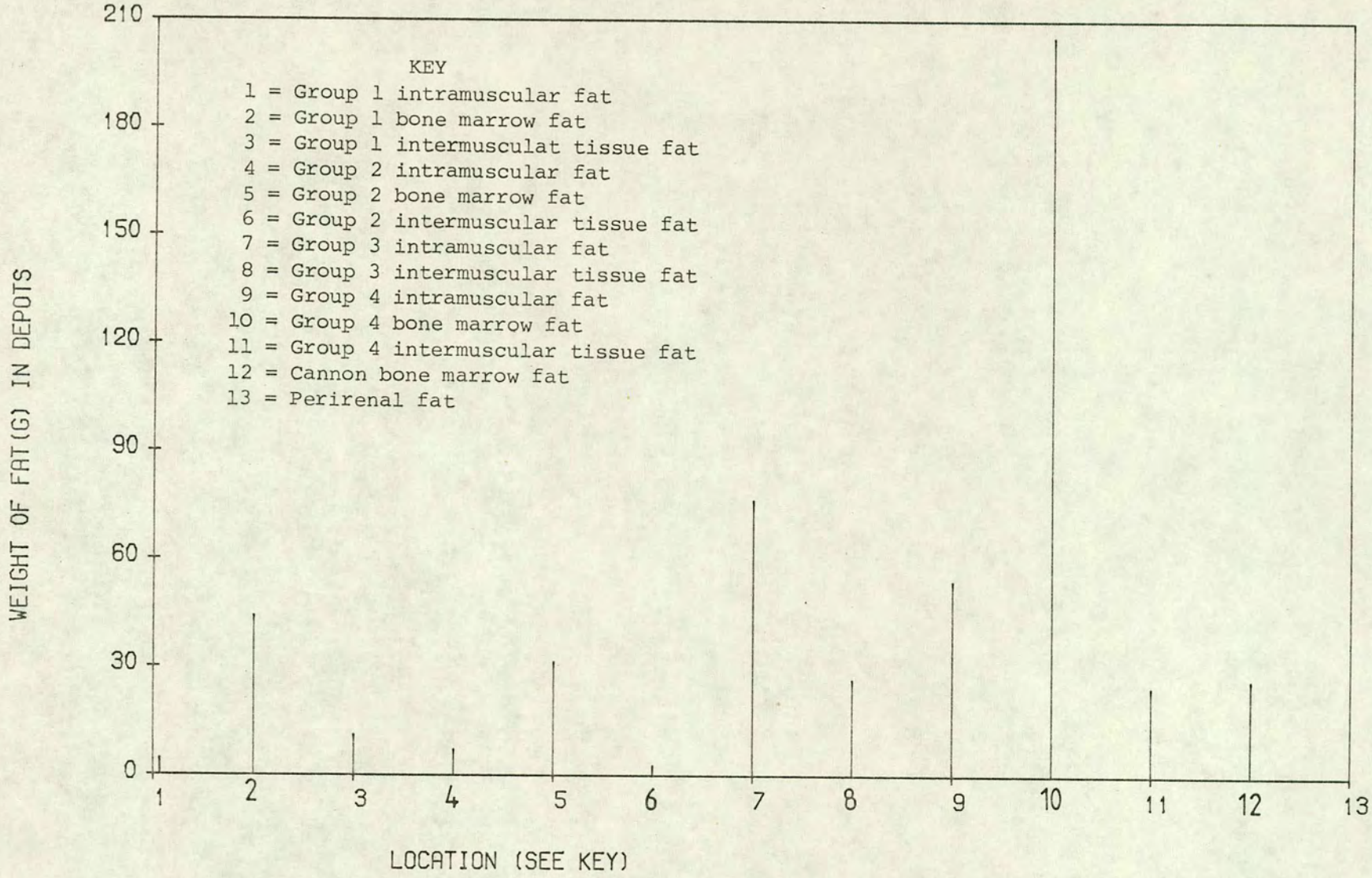


FIG.5.13.B FAT DEPOTS IN 1/2 CARCASS OF HIND 20.

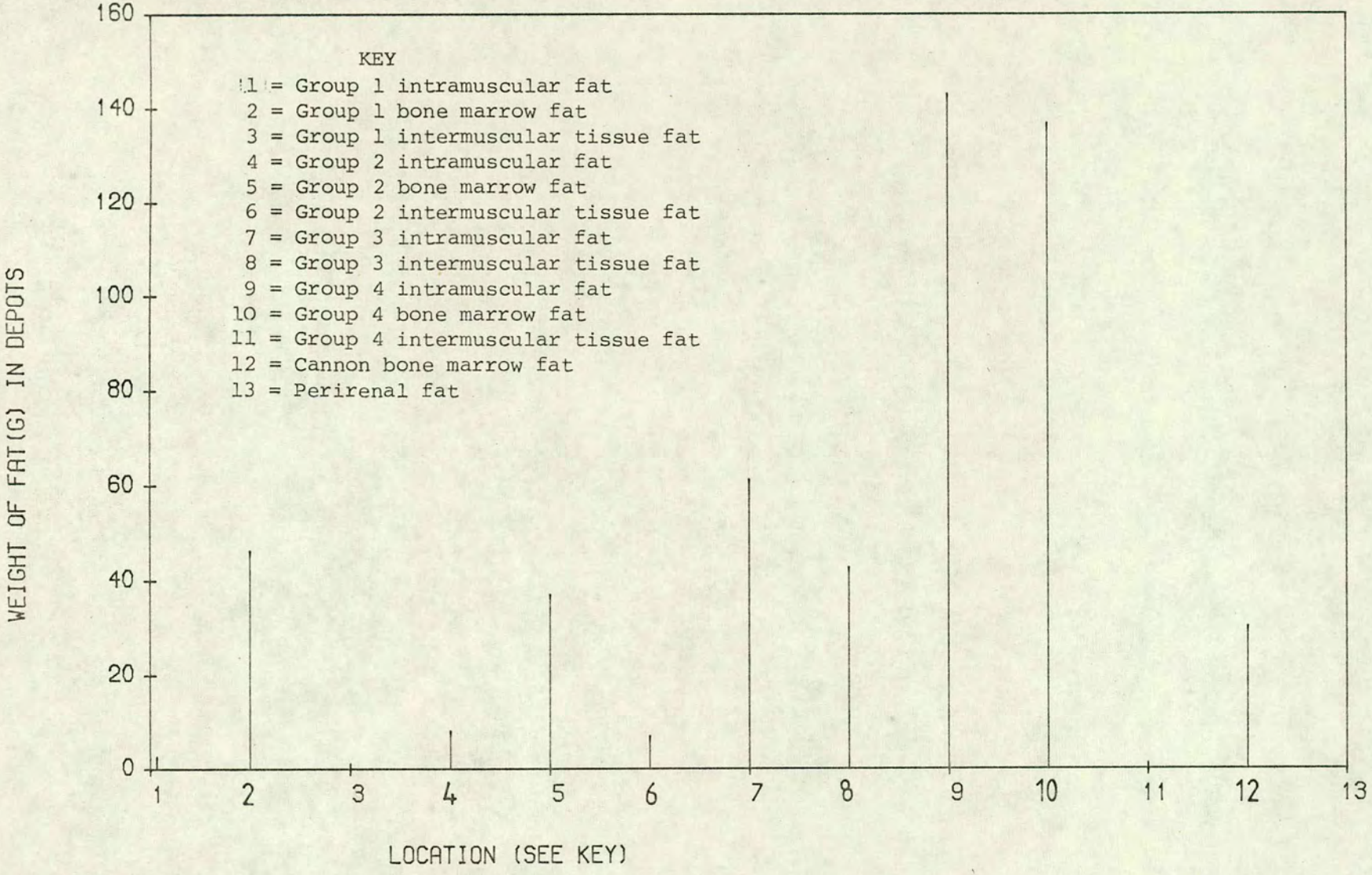


FIG.5.13.C FAT DEPOTS IN 1/2 CARACSS OF HIND 24.

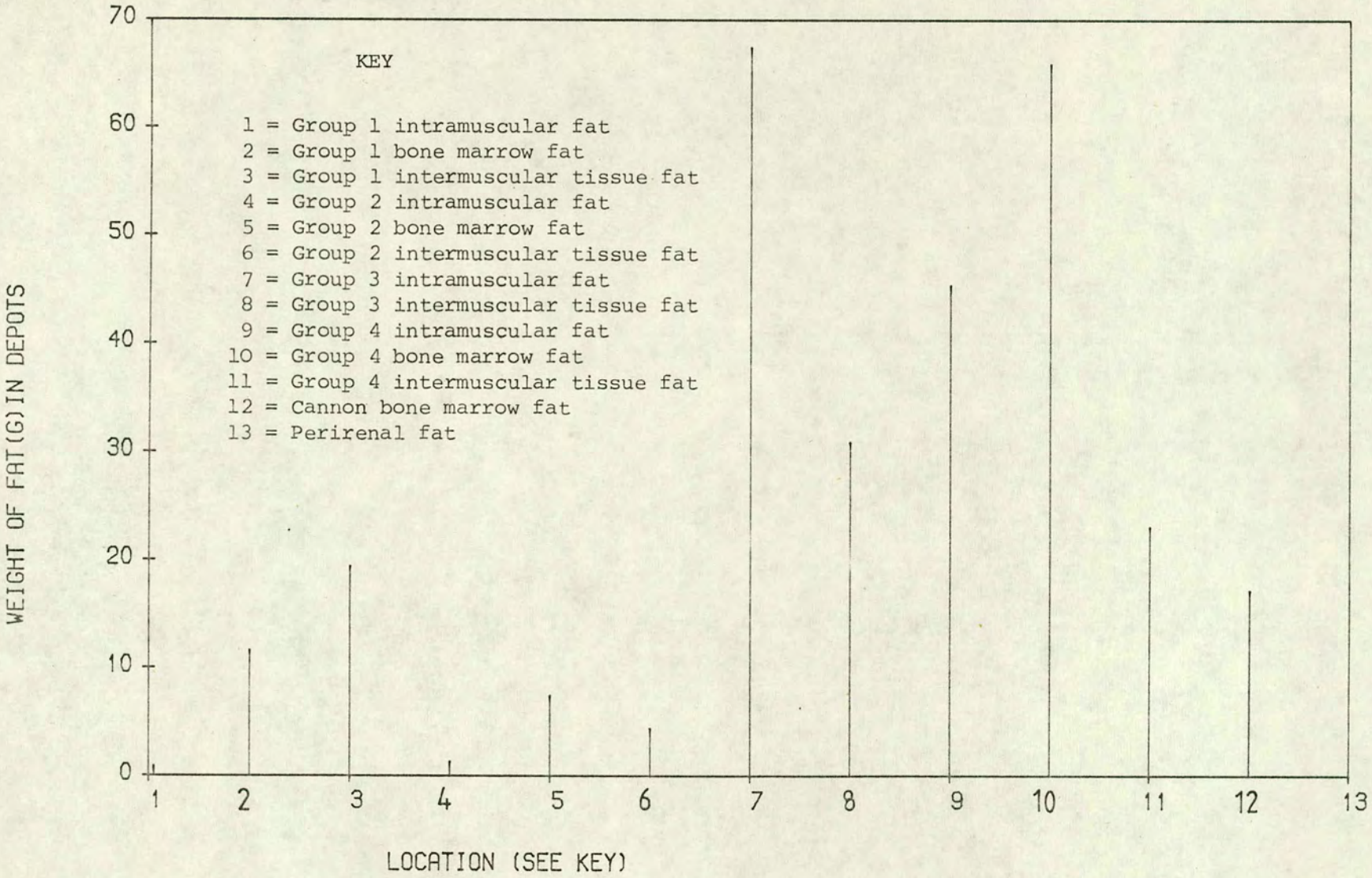


FIG.5.13.D FAT DEPOTS IN 1/2 CARCASS OF HIND 30.

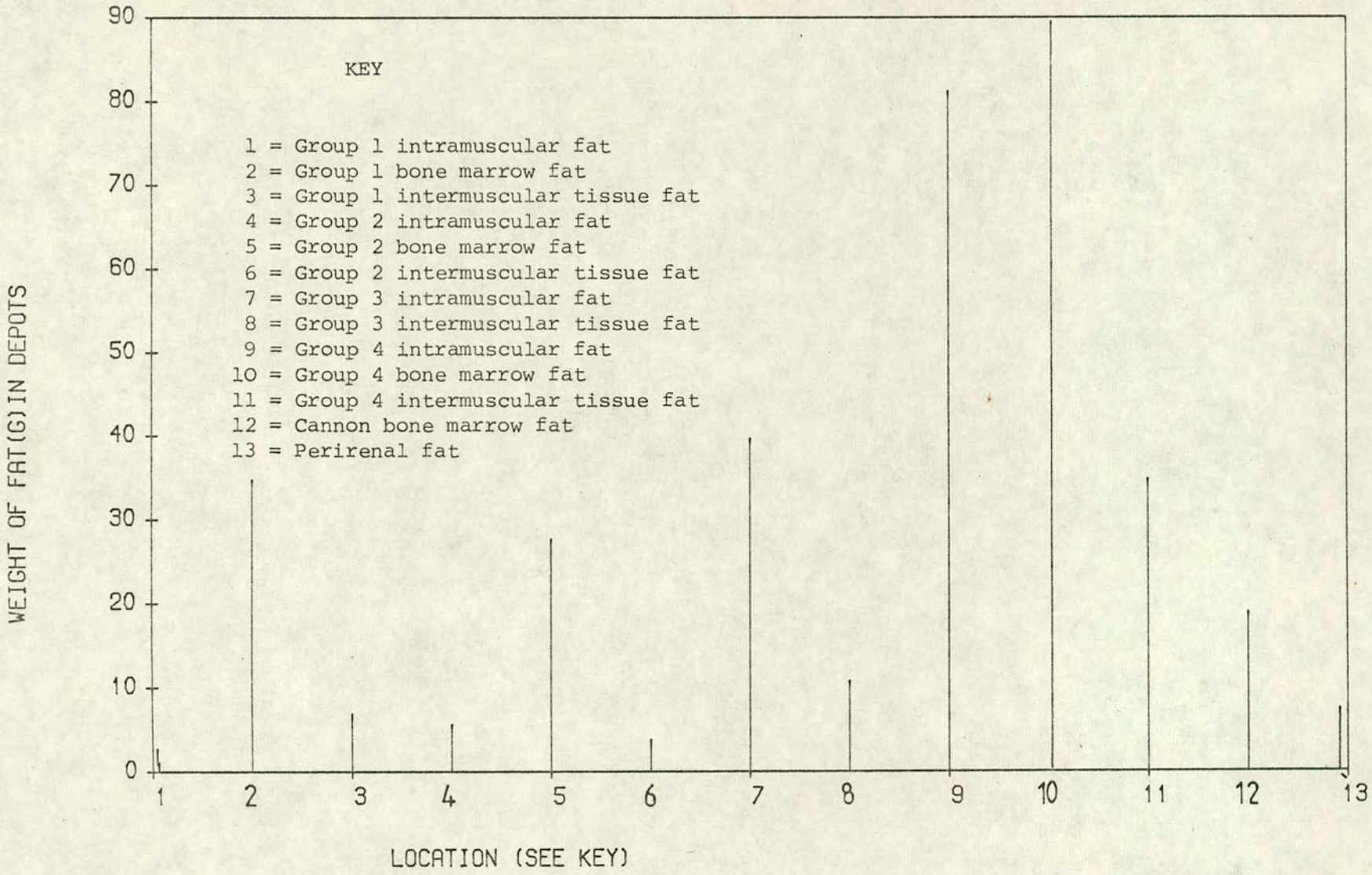


FIG.5.13.E FAT DEPOTS IN 1/2 CARCASS OF HIND 32.

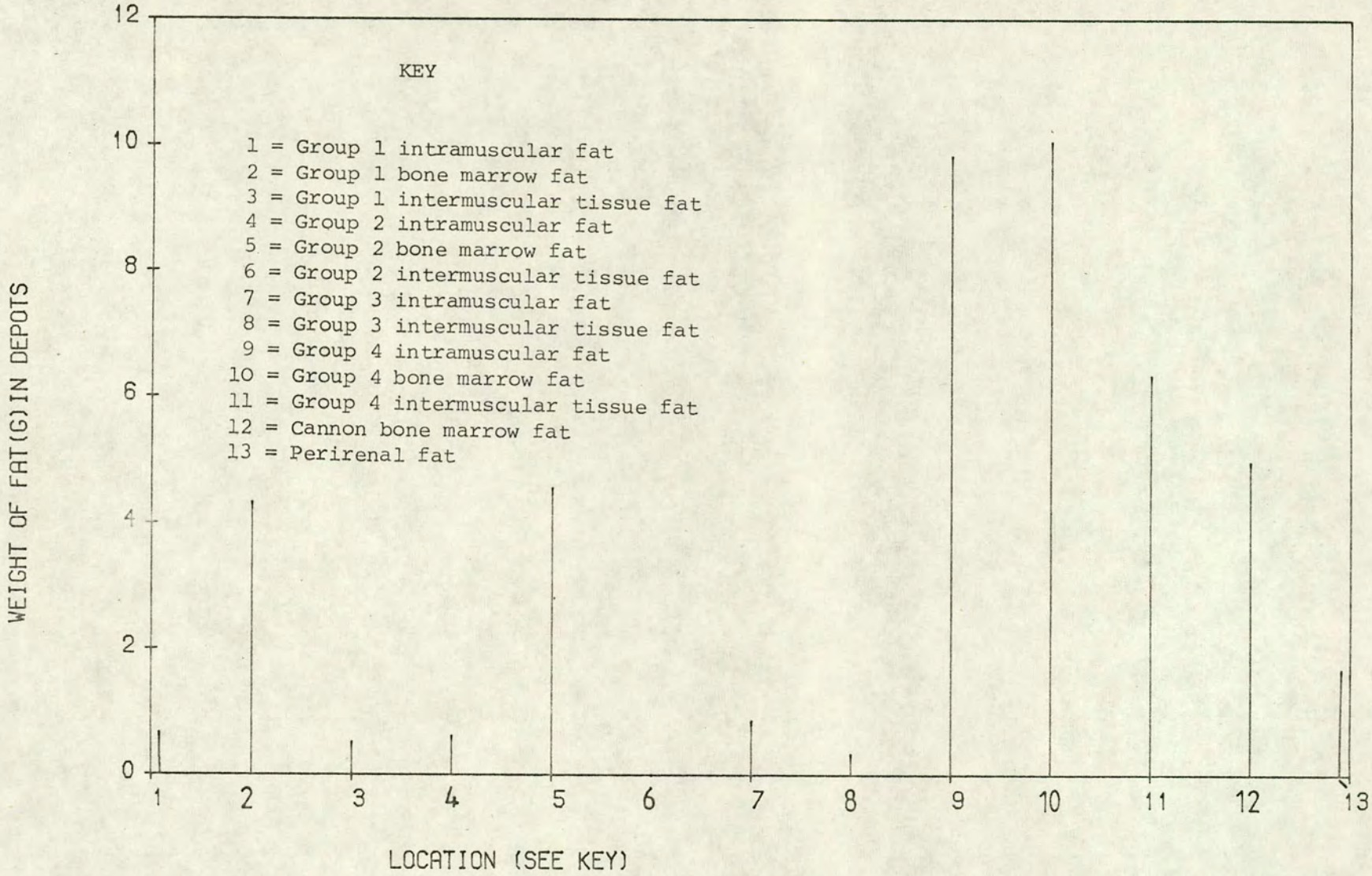


FIG.5.13.F FAT DEPOTS IN 1/2 CARCASS OF HIND 35.

fat) rather than in the body carcass, Within the half-carcass, the distribution of fat in mid-February appears to be:

kidney fat:	8%;
sub-cutaneous fat:	21%;
intermuscular tissue fat:	27%;
bone marrow fat:	16%;
intramuscular fat	28%.

This distribution within the half-carcass rapidly and drastically changes, so that by mid-March both sub-cutaneous and kidney dissectible fatty tissue have virtually, if not literally, completely disappeared from the bodies of many hinds: as can be seen in Table 5.6 and Figure 5.14, insufficient of either of these fatty tissues was present even to allow a sample to be taken for chemical determinations. Around this time intermuscular fatty tissue and intramuscular fat appear to be the major reserves. The weight of chemical fat held in the intermuscular tissues decreases rapidly compared to that contained in the muscle or in bone marrow, so that its contribution to the total chemical fat weight of the half-carcass is also decreasing.

By the end of May, chemical fat had almost completely disappeared from the carcass, and relatively little remained in the non-carcass, although by this point non-carcass chemical fat comprised 80% of that remaining in the body (see Figure 5.14). The distribution of chemical fat within the tissues of the half-carcass of the last hind collected (hind 35, on 25th May) was found to be:

kidney fat tissue:	4%;
sub-cutaneous fatty tissue:	9%;
intermuscular fatty tissue:	16%;
bone marrow fat:	43%;
intramuscular fat:	27%.

The sequence in which fat was mobilised appears to have been:

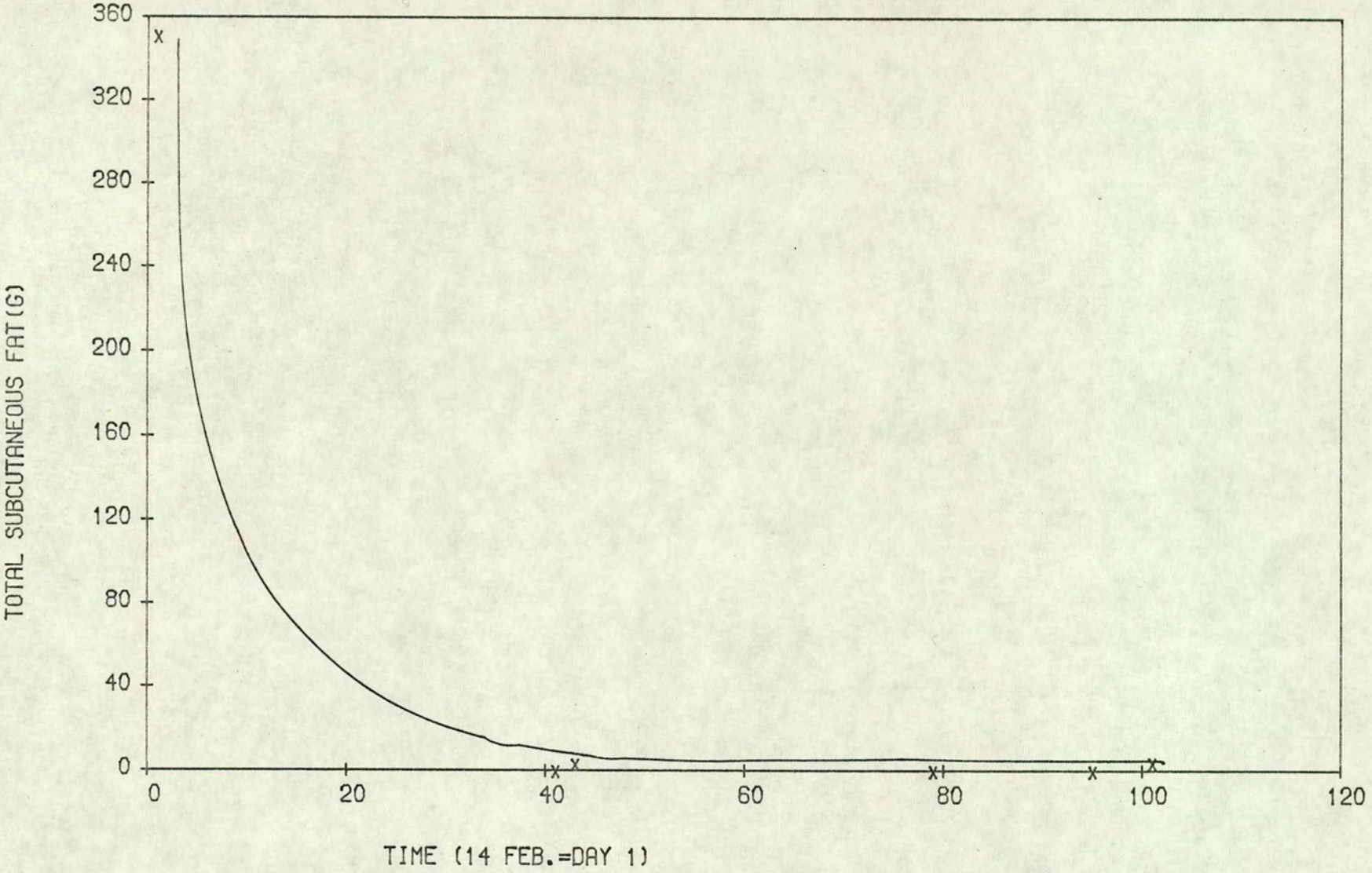


FIG.5.14.A 1/2-CARCASS SUB-CUT. FAT LOSS

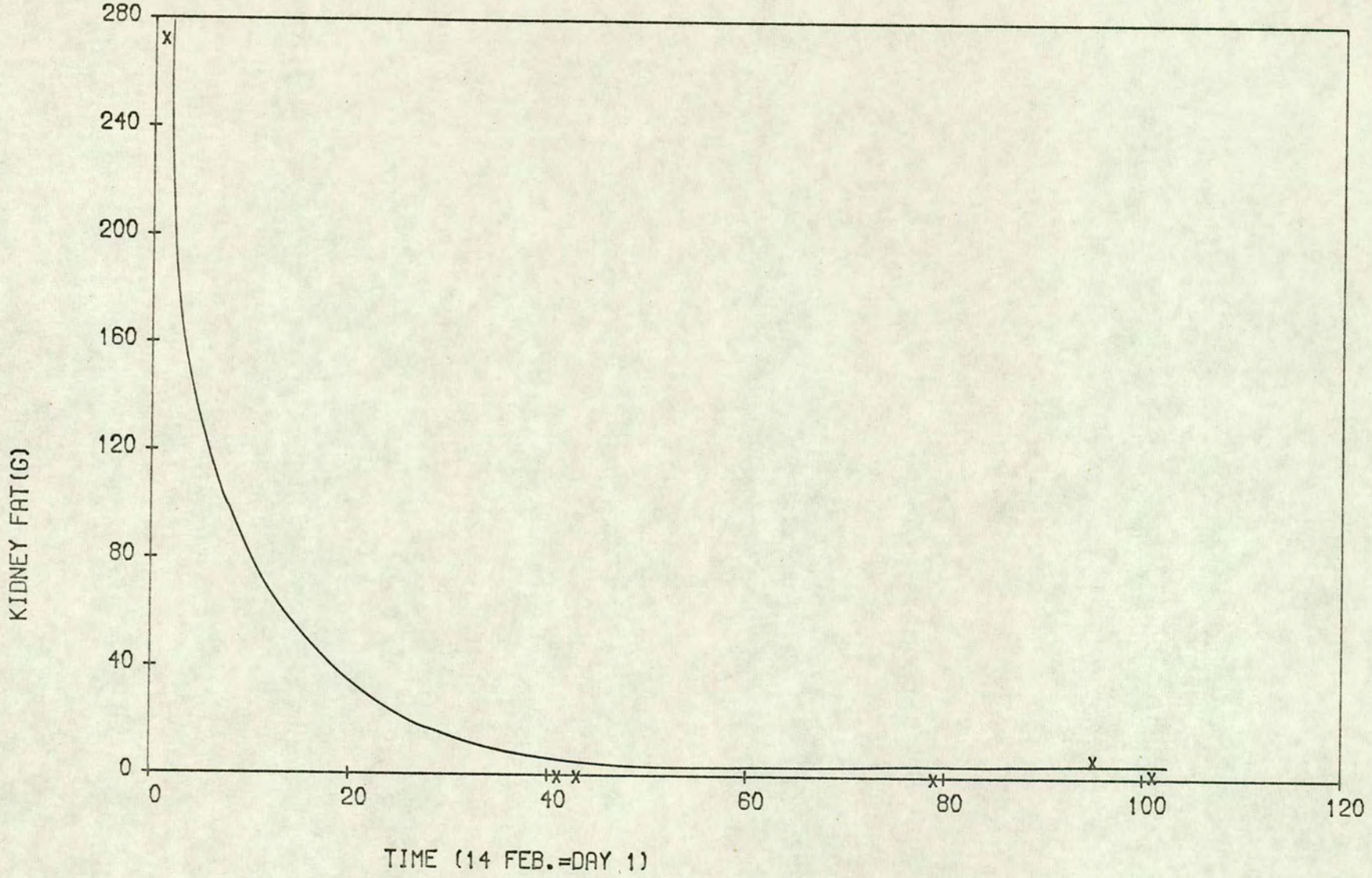


FIG.5.14.B KIDNEY FAT LOSS

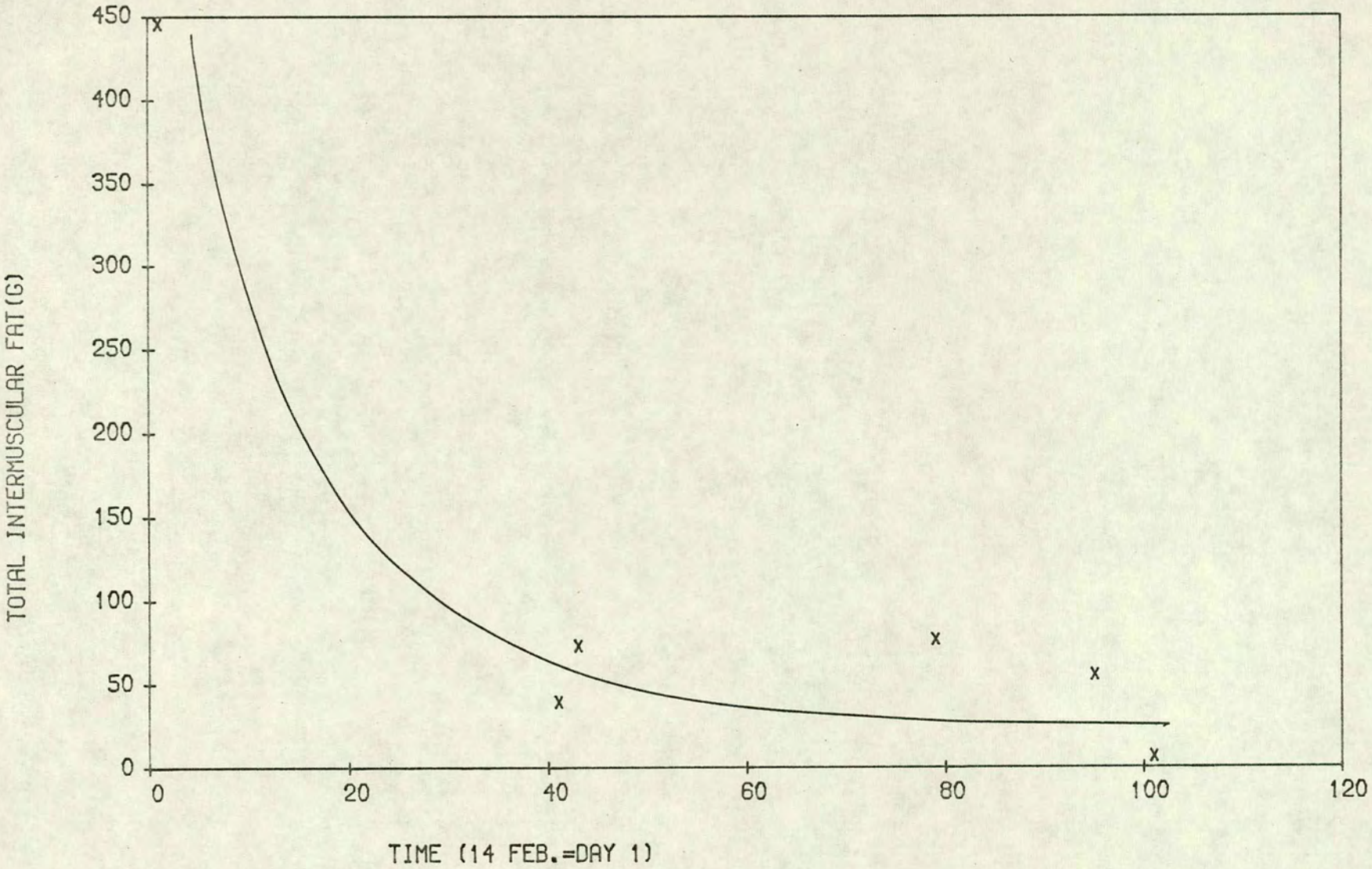


FIG.5.14.C INTERMUSCULAR FAT LOSS

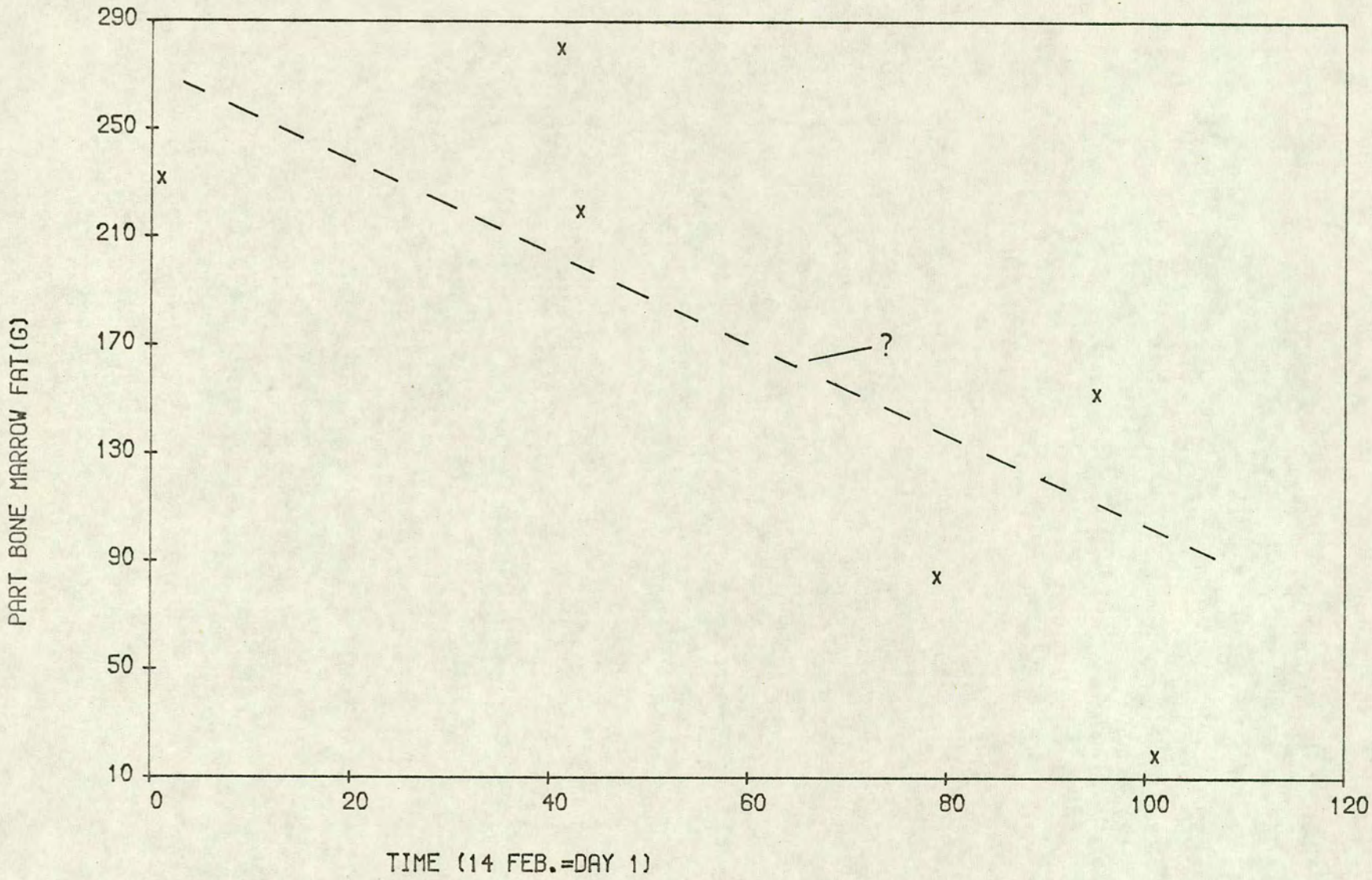


FIG.5.14.D BONE MARROW FAT LOSS

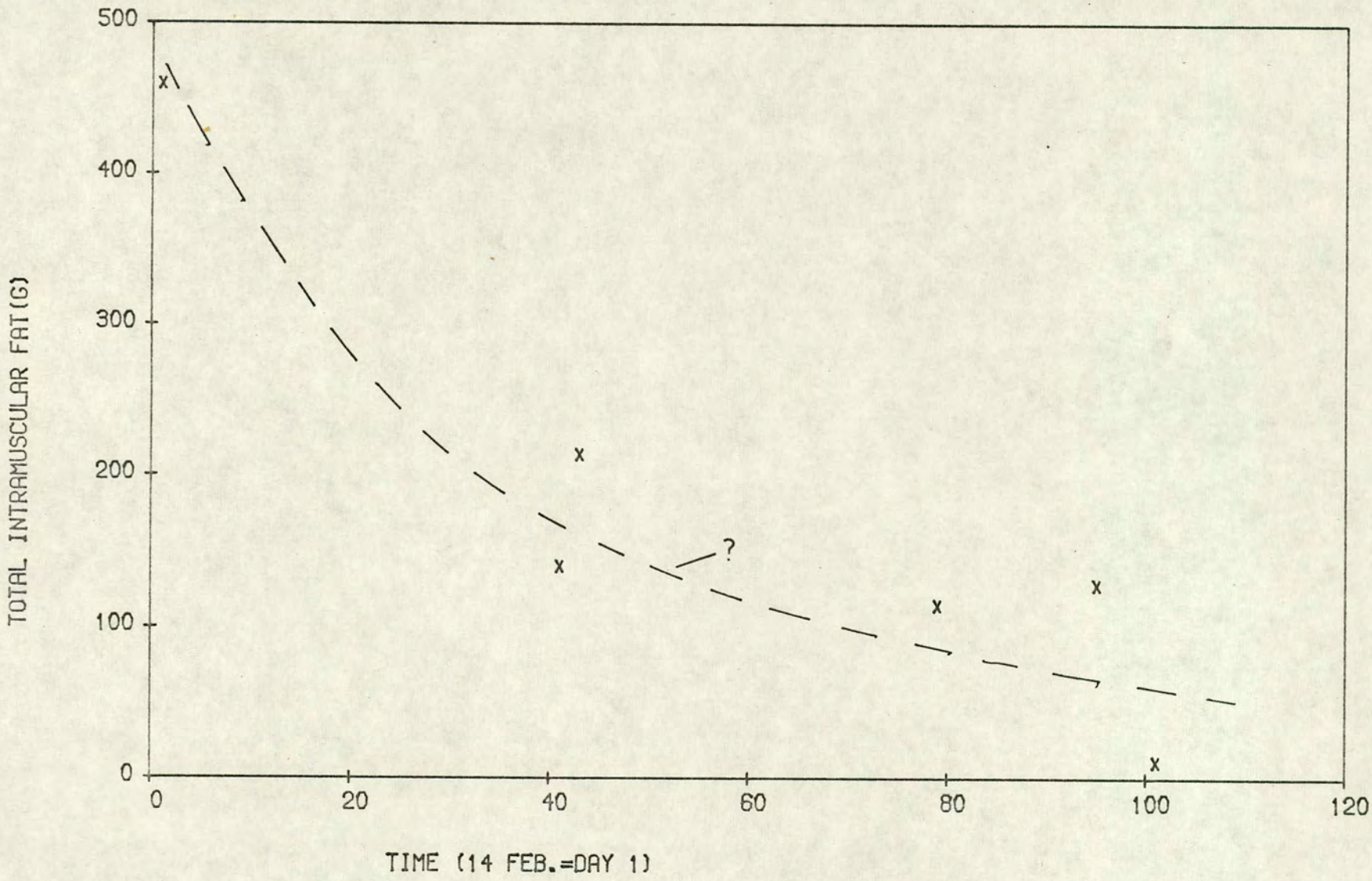


FIG.5.14.E INTRAMUSCULAR FAT LOSS

first sub-cutaneous fat, followed by kidney fat, followed by intermuscular fat, followed by intramuscular and bone marrow fat. However, it appears that it would be incorrect to view the mobilisation of fat as a consecutive process, so that no kidney fatty tissue fat is mobilised until all the chemical fat of the sub-cutaneous tissue has been consumed. Instead it appears that fat is being mobilised to some degree in all depots at any time, but that the rates at which this occurs differ so that, for instance, fat has disappeared from the sub-cutaneous tissue while it remains in the other depots of the body.

The pattern of fat distribution in the half-carcass of the six sub-sample hinds is somewhat different from that found in cattle by Johnson et al. (1972). Johnson and his colleagues found that intermuscular fat consistently contributed more to total half-carcass fat than did sub-cutaneous fat, both of which contributed more than did intramuscular. However, Johnson et al. only determined the weight of chemical fat in the muscle (i.e. intramuscular fat), comparing this to the weight of dissectible sub-cutaneous and intermuscular fatty tissues. Had they determined the weight of chemical fat in these tissues, it is possible that the size of the differences in the weights of intermuscular and of sub-cutaneous fat as compared to intramuscular fat, would have been found to decrease considerably.

The determinations made on the six sub-sample hinds demonstrate the importance of bone marrow fat to the internal energy regime of wild red deer hinds. It can be seen from Table 5.6 (a) and Figure 5.13 that although in February bone marrow fat comprises only around 13% of the total chemical fat in the body, by the end of May it by far is the major

remaining potential source of internally-provided energy.

5.6. Length of the period of negative energy balance.

The first hind to be analysed in this study was not collected until mid-February, so that by that time winter weight loss probably had already been occurring for a period of six to eight weeks, or even longer, What this loss will have consisted of can only be guessed at, but it seems likely that it will have been mostly of sub-cutaneous fat, some kidney fat, and also possibly of intermuscular fat; the rate of loss being greatest in sub-cutaneous, and least in intermuscular tissue. However, it has already been suggested that the mobilisation of chemical fat from the various depots appears to occur concurrently rather than consecutively.

From the analyses of the data from the bodies of all 19 hinds over the whole 100 day studied period, the suggestion was found that the rates of loss of empty-body weight, and of chemical fat and of protein weights from it, were not perfectly linear over the whole of the 100 days, but rather occurred at somewhat greater rates during the first half of the period. This suggestion is supported by the finding that the relationships between these weights and time were better described by their natural logarithms regressed against date, than are these relationships simply by the weights of the empty body, and the weights of fat and protein in it (see Table 5.7). It is interesting, however, that the loss of energy from the body does appear to occur linearly. Thus, although fat and protein weight losses seem to occur most rapidly prior to about the 1st of April, the loss of energy appears to continue to a steady rate (of around 8 kcal/kg

Table 5.7. Comparisons of regression equations and correlation coefficients describing the relationships between the passing of time and various weights of empty body and its components, the the relationships between time and the natural logarithms of these various attributes. The equation with the highest correlation is presumed to most resemble the real relationship.

$Y = 52.2 - 0.0836\ X$ (Y = empty-body weight in kg)	$r = -0.5140$	$P < 0.05$	$t = 2.4706$
$Y = 3.957 - 0.0018\ X$ (Y = natural log. E-B weight)	$r = -0.5189$	$P < 0.05$	$t = 2.5027$
$Y = 5.949 - 0.0504\ X$ (Y = chemical fat in E-B in kg)	$r = -0.9111$	$P < 0.001$	$t = 9.1124$
$Y = 2.106 - 0.0211\ X$ (Y = natural log. chemical fat weight)	$r = -0.9249$	$P < 0.001$	
$Y = 11.666 - 0.0321\ X$ (Y = estd. protein in E-B in kg)	$r = -0.6481$	$P < 0.05$	$t = 3.5085$
$Y = 2.4643 - 0.0023\ X$ (Y = natural log. protein weight)	$r = -0.6522$	$P < 0.05$	$t = 3.5470$

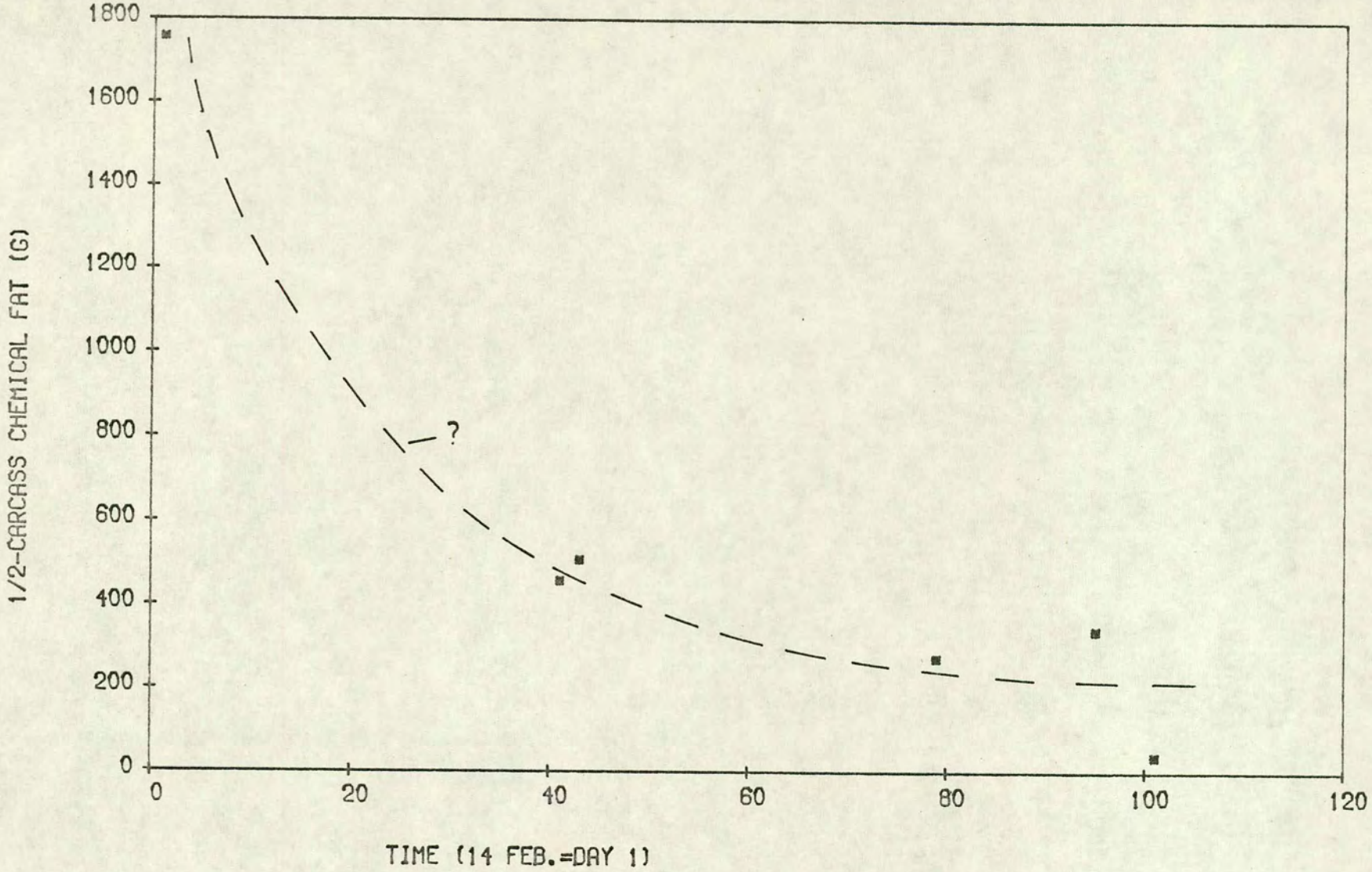


FIG.5.15 LOSS OF 1/2-CARCASS CHEMICAL FAT

empty-body weight) over the whole of the period mid-February to the end of May.

The hind sample of 19 animals unfortunately is too small to indicate at what point the losses of body and of fat weight, and of energy from the body, cease to occur. Mitchell et al. (1976) have found that both yeld and milk hinds on the Isle of Rhum reach their minimum body weights, and indices of their condition (i.e. kidney/fat weight ratios, weights of kidney fat and weights of "rump" - haunch subcutaneous and possibly intermuscular-fat), in 'March or April-May': the carcass weights of their yeld hind sample were lowest at around the end of April or the beginning of May. However, since they did not collect their next hinds until early July, the nadir of hind weights and condition indices may have occurred at some time in May or early June (or even in early April). When hinds are poorest in condition, after which they begin to put on fat and improve (if they have not died) almost certainly varies from year to year, and from one area of the Highlands to another. Unfortunately, it is not possible yet to say whether the occurrence of good weather and the early onset of new vegetative growth can supply sufficient dietary energy, in spite of the ever-increasing energy demand of the growing foetus, to enable hinds to begin to improve in condition before parturition. It has already been pointed out that although the rate of body weight loss in the 19 hinds of the present study appears to have been decreasing by around the beginning of April (see Table 5.7), the rate of loss of energy from the conceptus-free bodies of the hinds appeared to continue right up until the last hinds were collected at the end of May. However, the limited data available from the 6 hinds

chemically analysed in detail seem to indicate that at least some hinds can begin to improve in condition while still pregnant: the reappearance of kidney fat in hinds 32 and 35, and of haunch sub-cutaneous fat in hind 35, appears to suggest that these hinds had already (by late May) begun to improve in condition and deposit new body fat although their calves had not been born yet.

Clearly research into the energy contents and digestibilities of the major species of vegetation grazed by red deer, and how these factors change over the year, is required before this matter can be fully understood. It is of particular importance, since such knowledge is required before intelligence management can be applied to increase red deer productivity (for instance by provision of artificial feeding, or by improving the quality of grazing available).

CHAPTER 6. Compositional Development of the Collected Foetuses.

One of the objectives of the research reported on in this thesis was to attempt to establish the nutritional cost of pregnancy for wild Scottish red deer. To do so precisely, the energy and nutrients deposited in all the products of conception (i.e. the uterus, uterine fluids and mammary gland, as well as those in the foetus itself), and the efficiency of the processes by which they were deposited, would have to be known. To establish the efficiency of energy use, a difficult experiment would have to be carried out over the whole of gestation on live, captive animals. Furthermore, when the collecting was in progress, I had not given sufficient thought to what would have to be measured, to establish even the energy content of the products of conception. Thus, not only did I not collect samples of uterine fluids, so that their contents could be determined, but also I minced both the mammary glands and uteruses of the hinds in with the offal Group of body components, instead of determining their contents separately. Fortunately, the very considerable similarity found between the compositional development of the collected foetuses and that of white-tailed deer, suggests that the energy contents of the whole gravid uteruses of the collected hinds can be well-estimated by an equation derived from white-tailed deer (Robbins and Moen, 1975; see section 6.4 of this chapter).

The growth in weight of the collected foetuses and the accumulation of foetal energy, DM and major mineral nutrients, in relation both to foetal size, and to time, are reported in this chapter, and are compared to the findings of the study

by Robbins and Moen on white-tailed deer. The cost to a hind, in terms of energy and nutrients, of producing a calf is discussed in Chapter 7.

6.1 A brief description of the foetuses collected.

A total of 30 red deer foetuses were collected for study during this research. One foetus unfortunately was lost during transportation to Edinburgh, so that the examined sample population consisted of only 29 foetuses. The places and method of collection and of preparation for chemical analysis are described in Chapter 2. The foetuses in fact were dissected and a study made of the growth of internal organs, but this was not a direct part of the present thesis, and is the subject of a separate paper (Anderson and MacDonald, in press).

The first 11 foetuses of the sample were collected from Glen Feshie estate during the latter half of January 1973. The last 18 foetuses collected were taken from the 19 hinds described in previous chapters (the foetus of hind 28 was lost). Because they were taken from wild animals, the precise ages of the collected foetuses are not known. However, from a study of conception dates at Glen Feshie, Mitchell and Lincoln (1973) have estimated that the median conception date (by hinds in the year of their study) was the 19th of October. It seems reasonable to assume that the median date of conception in 1972 (when the foetuses, collected for this study, were conceived) was not greatly different from this at Glen Feshie, and probably was roughly similar at both Killilan and Corrour. If this be so, since average gestation length of Scottish hinds appears to be

around 233 days (Guinness et al., 1971), it is probably legitimate to assume that the majority of the first 14 foetuses collected were in the middle, and the majority of the last 15 collected, in the final third, of the gestation period. The foetus of the last hind collected (hind 35, taken at Corrour on 25th May) appeared (judging by its weight) to have been within a week of term, although the foetus of hind 34, collected the same day, did not appear to be so near birth.

6.2 Growth in weight, energy content, protein and fat.

6.2.1 FOETAL WEIGHT.

The weights (measured on removal from the uterus) of the collected foetuses are shown in Table 6.1 and Figure 6.1.A. Foetal weight did not begin to increase rapidly until the beginning or middle of February (at around 105 days from the 19th October, or slightly less than half way through the assumed gestation period), and the greatest rate of increase occurred after around the middle of March (i.e. during the assumed last third of gestation). Figure 6.1.B shows that, in common with the developing foetuses of placental mammalian species (Huggett and Widdas, 1951), the increase in foetal weight over the whole period of collection (18 January to 25 May) is well described by a simple linear regression of the cube root of foetal weight against time (where 18 January = Day 1).

6.2.2 INCREASE IN THE DM CONTENTS OF THE FOETUSES.

The weight of DM in the foetuses (as estimated by multiplication of the percentage of DM found in the sub-samples by weight of the intact foetus) increased over the collection

DATE (18 JAN=DAY 1)	FOETAL WEIGHT (G)	FOETAL DM WEIGHT (G)	FOETAL DM (%)	FOETUS ENERGY CONTENT(KCAL)
1.0000	400.0000	54.4000	13.6000	241.8700
1.0000	220.0000	30.5800	13.9000	124.3500
5.0000	434.0000	57.2880	13.2000	261.2200
5.0000	272.0000	35.3600	13.0000	152.6200
5.0000	210.0000	26.2500	12.5000	117.0600
5.0000	260.0000	34.8400	13.4000	152.5000
5.0000	145.0000	19.8650	13.7000	81.7800
6.0000	311.0000	49.7600	16.0000	219.2600
7.0000	378.0000	49.1400	13.0000	215.7900
7.0000	232.0000	28.7680	12.4000	130.3900
12.0000	320.0000	40.9600	12.8000	183.1500
28.0000	550.0000	88.5499	16.1000	383.6499
49.0000	335.0000	57.9549	17.3000	248.9700
49.0000	436.0000	59.7320	13.7000	267.1599
68.0000	1664.0000	301.1836	18.1000	1340.7500
68.0000	2145.0000	386.0999	18.0000	1771.9700
68.0000	2250.0000	368.9998	16.4000	1666.0698
70.0000	1078.0000	187.5719	17.4000	816.7100
70.0000	1815.0000	339.4048	18.7000	1461.8799
70.0000	2195.0000	408.2695	18.6000	1872.4500
70.0000	2115.0000	376.4695	17.8000	1741.5098
71.0000	2240.0000	389.7598	17.4000	1743.4700
72.0000	2628.0000	483.5515	18.4000	2162.6299
106.0000	4933.0000	1055.6616	21.4000	5194.2773
107.0000	3762.0000	790.0198	21.0000	3422.1899
112.0000	3524.0000	669.5598	19.0000	3062.5698
112.0000	4950.0000	1079.0994	21.8000	4741.4570
128.0000	6005.0000	1363.1345	22.7000	6039.5078
128.0000	4720.0000	1076.1592	22.8000	4905.7773

16 GO :

Table 6.1.(a). The weights of the collected foetuses and their dry matter and gross energy contents.

DATE (18 JAN=DAY 1)	FOETAL FAT WEIGHT (G)	FOETAL FAT (% IN DM)	NITROGEN (% IN DM)	ESTIMATED PROTEIN WEIGHT (G)
1.0000	2.2630	4.1600	9.1050	30.9570
1.0000	1.8103	5.9200	8.5770	16.3928
5.0000	2.9561	5.1600	9.6190	34.4408
5.0000	1.9519	5.5200	8.4150	18.5971
5.0000	1.6170	6.1600	8.7690	14.3866
5.0000	1.8953	5.4400	8.3790	18.2452
5.0000	1.1919	6.0000	8.5910	10.6662
6.0000	2.8463	5.7200	8.4780	26.3665
7.0000	2.6536	5.4000	8.5830	26.3605
7.0000	1.5995	5.5600	8.9840	16.1532
12.0000	2.1955	5.3600	8.7160	22.3129
28.0000	4.6754	5.2800	8.7470	48.4091
49.0000	2.7587	4.7600	9.3320	33.8022
49.0000	2.7477	4.6000	9.1800	34.2712
68.0000	12.8907	4.2800	9.5960	180.6348
68.0000	20.8494	5.4000	9.7740	235.8585
68.0000	18.7452	5.0800	9.7860	225.6894
70.0000	10.4290	5.5600	9.7200	113.9498
70.0000	20.0928	5.9200	9.5770	203.1548
70.0000	26.7825	6.5600	10.0690	256.9287
70.0000	22.4376	5.9600	10.3590	243.7402
71.0000	23.5415	6.0400	10.2540	249.7871
72.0000	31.9144	6.6000	9.9500	300.7083
106.0000	70.9404	6.7200	10.7080	706.5012
107.0000	33.1808	4.2000	9.4380	466.0125
112.0000	42.5840	6.3600	9.2910	388.8047
112.0000	62.1561	5.7600	10.6190	716.1843
128.0000	71.9735	5.2800	10.6960	911.2546
128.0000	70.1655	6.5200	11.3990	766.6956

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Table 6.1.(b). The weight of chemical fat and estimated weight of protein (weight of N x's 6.25), and percentages of fat and nitrogen in foetal dry matter.

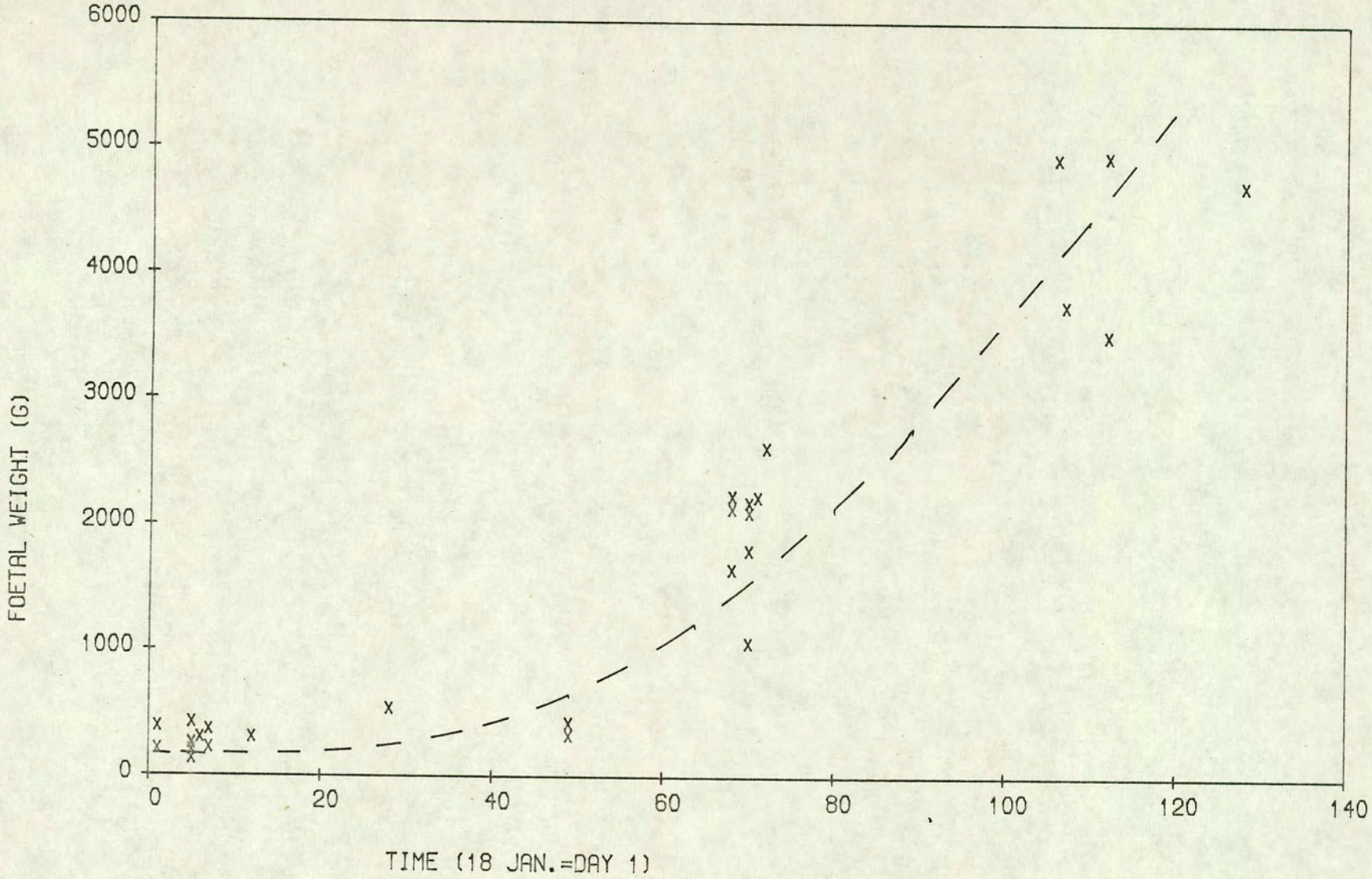

FIGURE 6.1.A. INCREASE IN FOETAL WT.

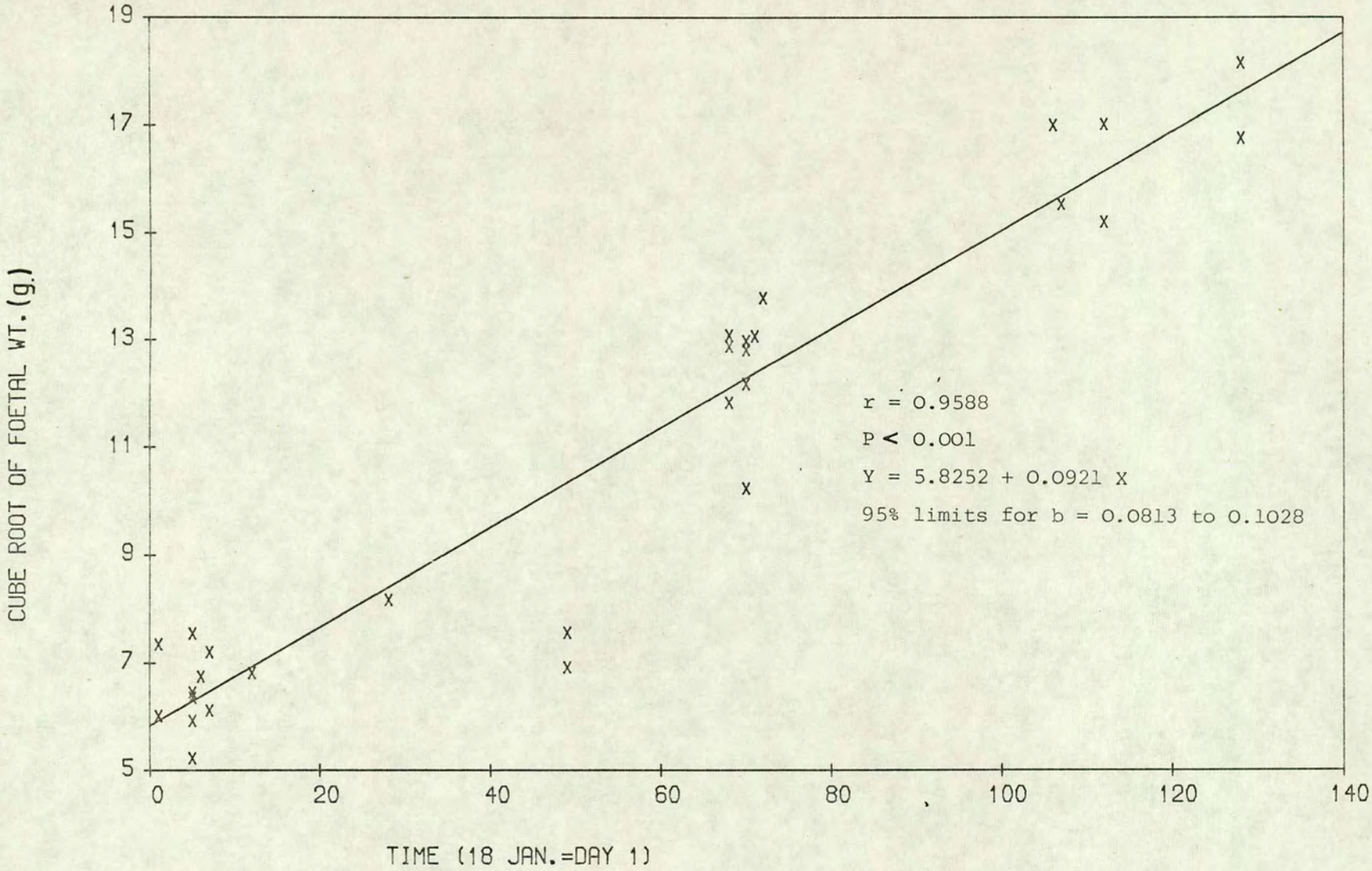

FIGURE 6.1.B. (FOETAL WT.)**0.33 VS. TIME

period in a curvilinear manner similar to that of gross foetal weight (Figure 6.2; Table 6.1). The percentage of DM in the weights of the foetuses increased both as time passed (Figure 6.3) and as foetal weight increased (Figure 6.4). At the beginning of the (presumed) middle of the gestation period foetuses weighed from 100g to 300g, around 87% of which was water. Near the end of gestation water content had fallen to around 77%. However, it can be seen from Figure 6.4 that the rate of increase in the percentage of foetal weight that is DM does not appear to have beenllinear over the whole period, but rather to have increased more rapidly in the earlier part of the collection period, and begunto slow down by the time the foetus reached a weight of around 2.0 kg.

6.2.3 INCREASE IN FOETAL GROSS ENERGY CONTENT.

The energy content (in kcal) per g of foetal DM rose (over the 128 days that foetuses were collected) in a manner similar to gross foetal weight and weight of foetal DM (Table 6.1; Figure 6.5). The energy per g of DM of the foetuses was almost perfectly linearly correlated with the increase in foetal weight ($r = 0.992$ $P < 0.001$; see Figure 6.6.A); an increase in foetal DM weight of 1g contained around 0.9970 kcal of energy. The gross energy content of the foetuses increased over the period of collection as shown in Figure 6.6.B. The two regression lines shown in the figure estimate the average daily increase in foetal gross energy content during the first and second halves of the collection period as: approximately 2.6 kcal gain per day up until about the 15th of March; and approximately 64.1 kcal gain per day from then until birth.

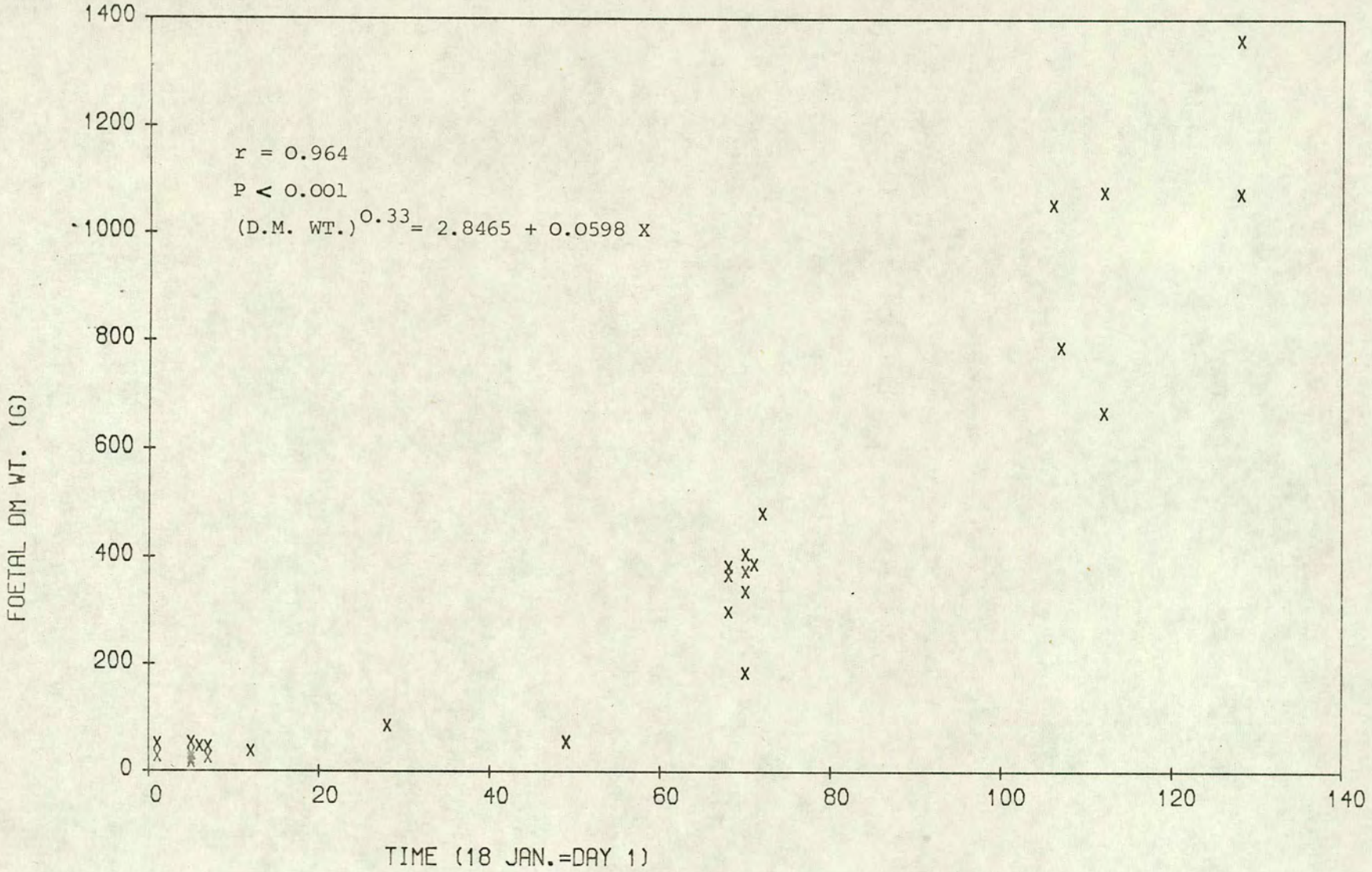

FIGURE 6.2. INCREASE IN FOETAL DM WEIGHT

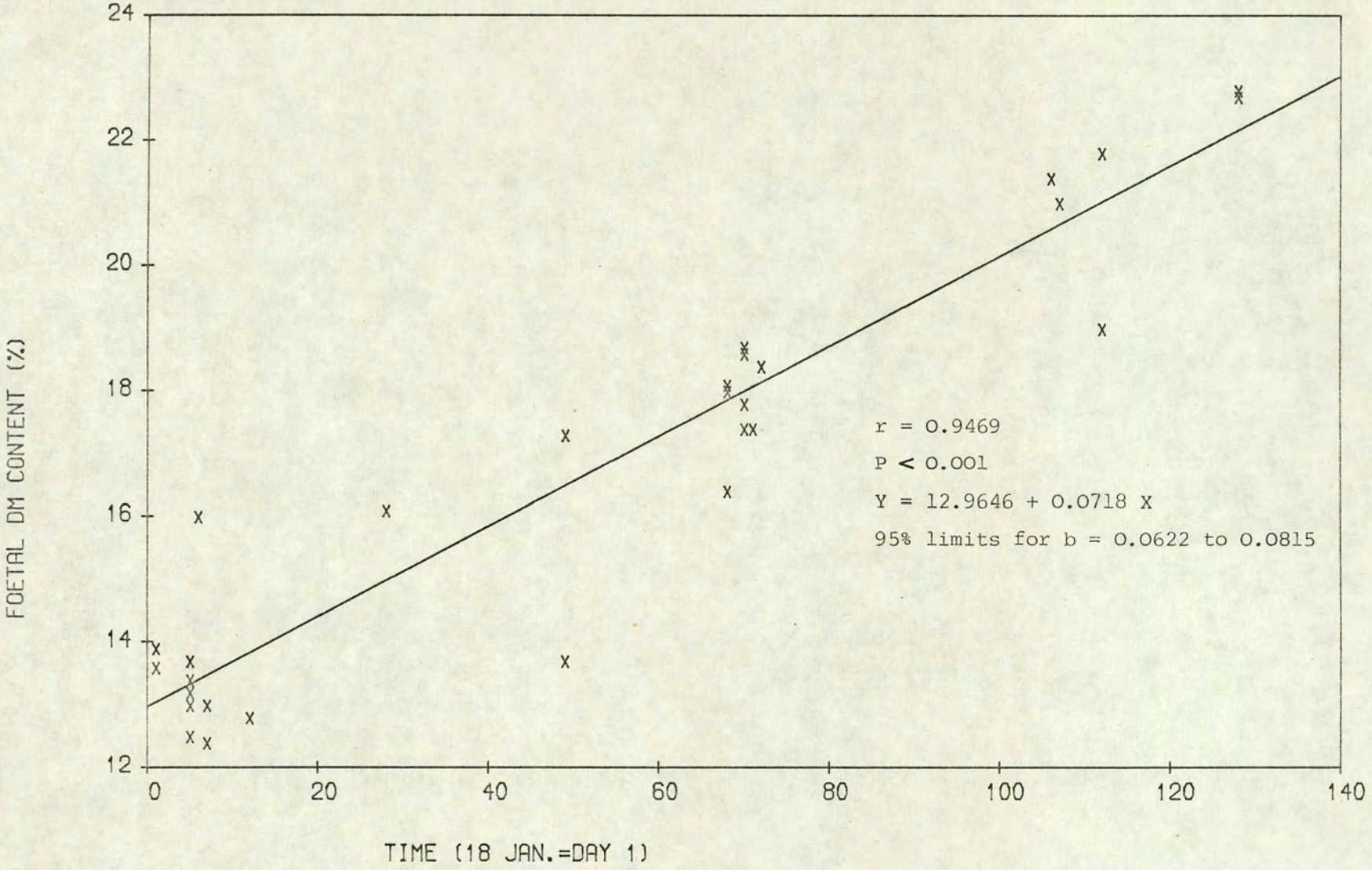

FIGURE 6.3. FOETAL DM CONTENT (%)

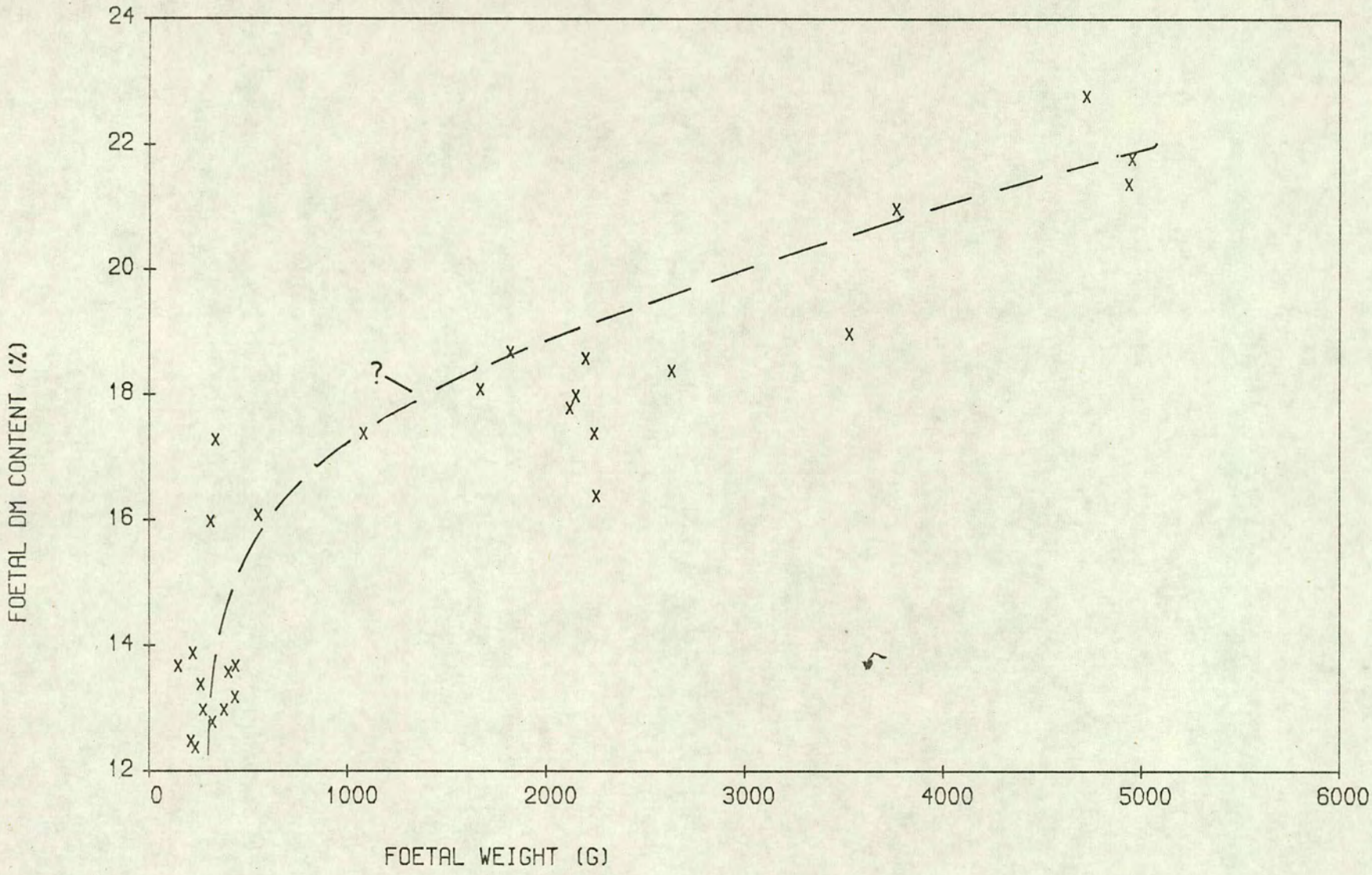

FIGURE 6.4. RISE IN % FOETAL DM

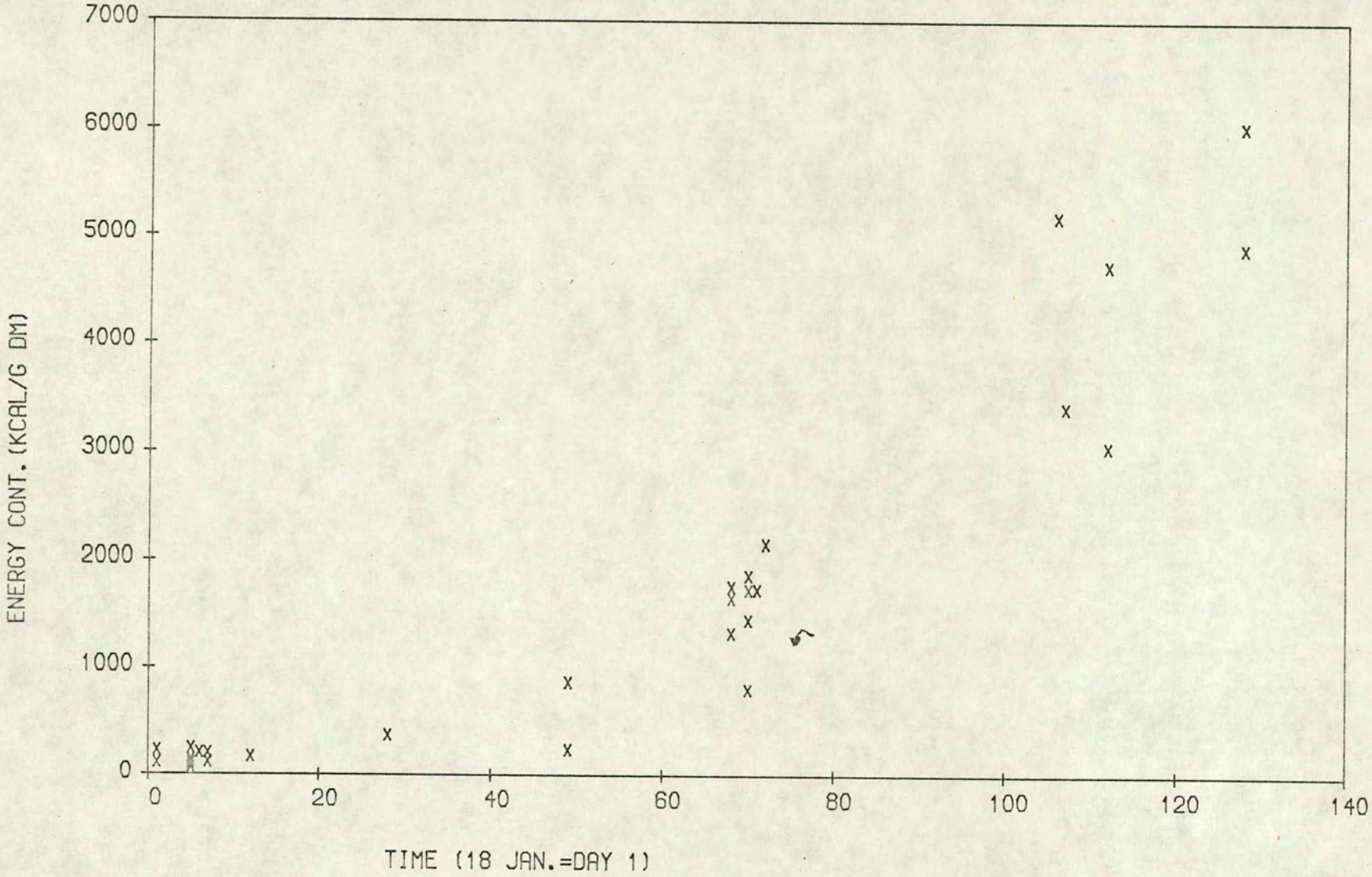

FIGURE 6.5. FOETAL ENERGY VS. TIME

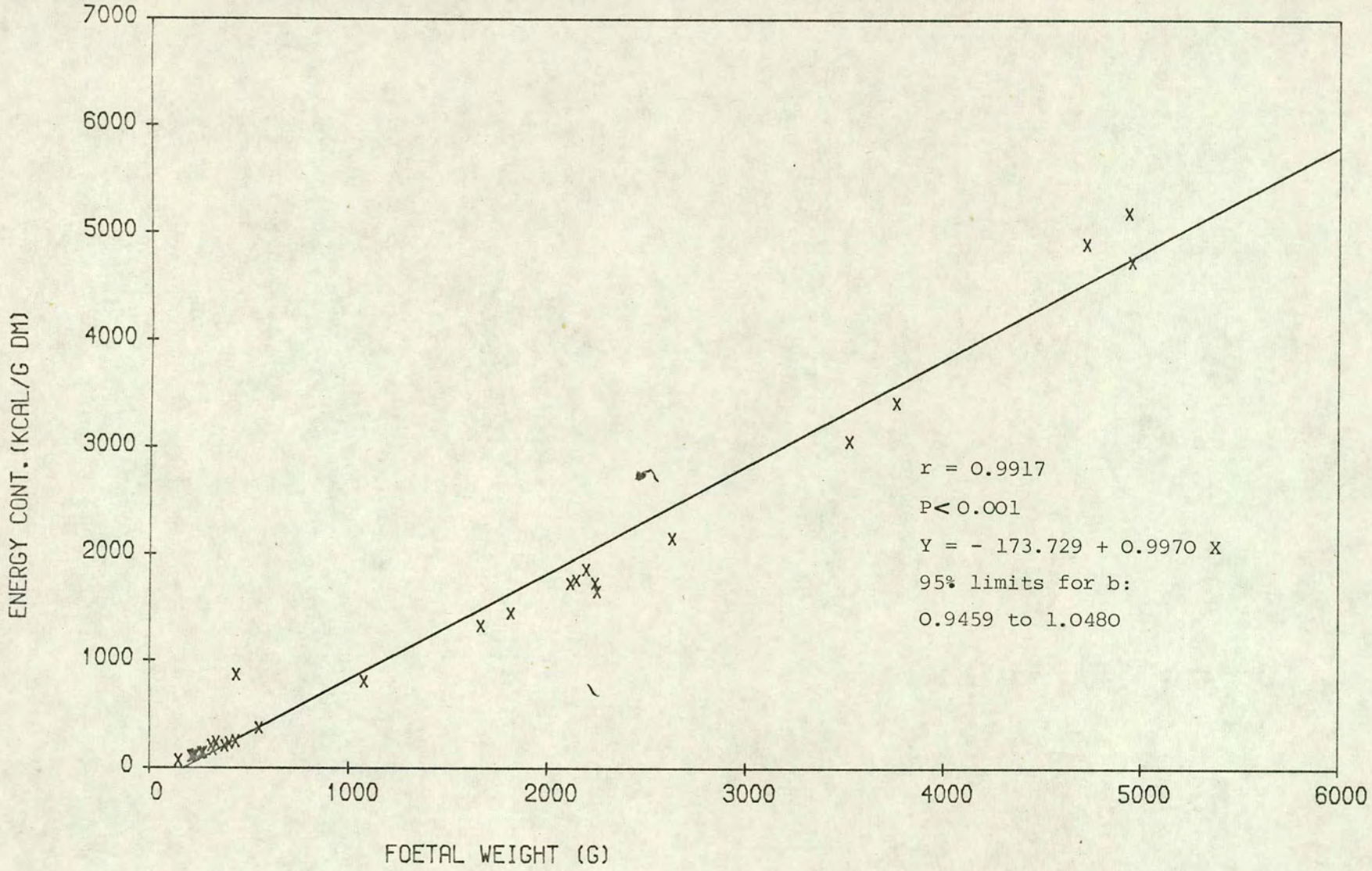

FIGURE 6.6.A. ENERGY CONT. VS. WEIGHT

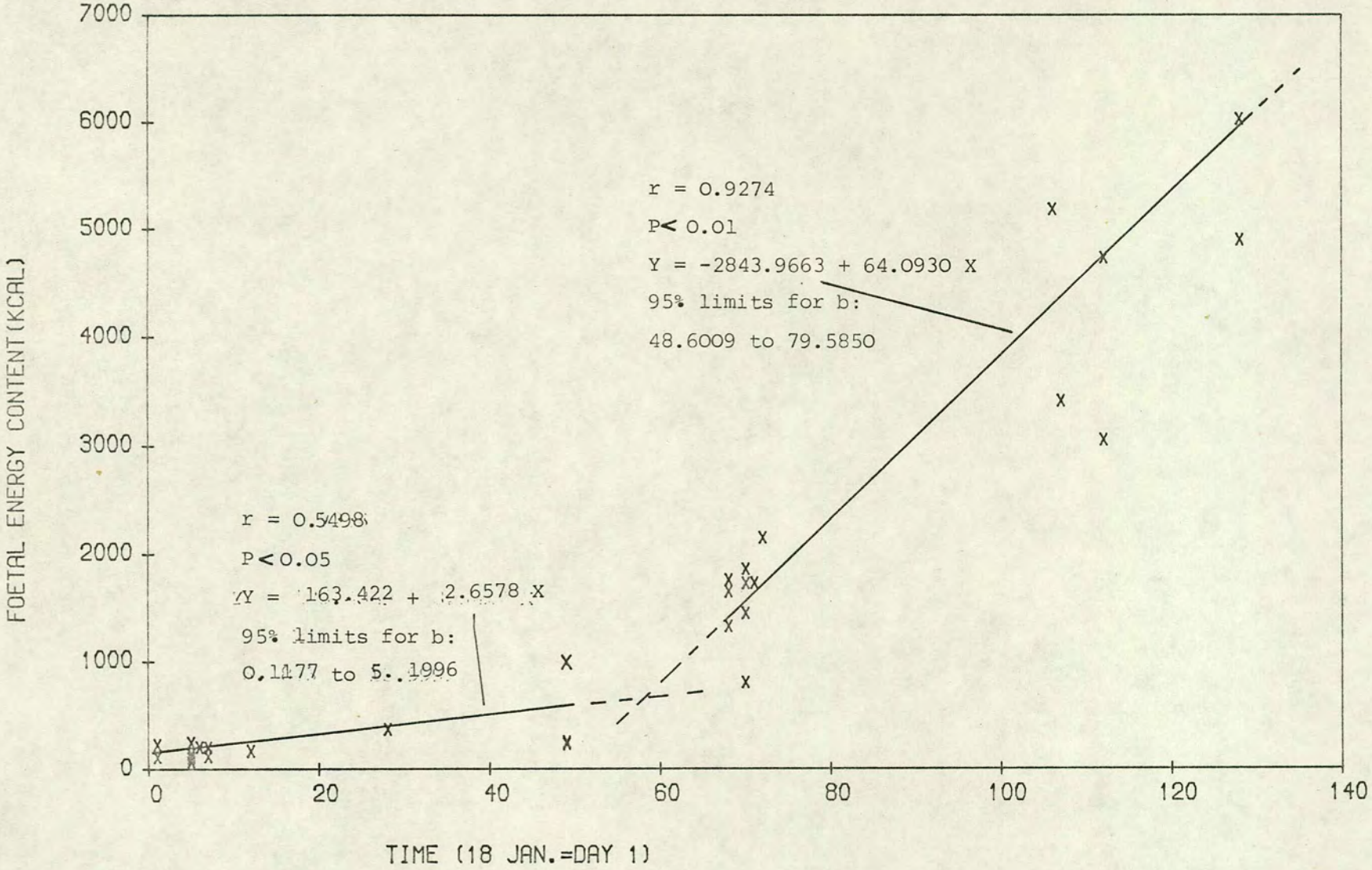

FIGURE 6.6.B. FOETAL ENERGY CONTENT GAIN

6.2.4 INCREASE IN FOETAL PROTEIN CONTENT.

The weight of protein in the collected foetuses (estimated by multiplying weight of foetal nitrogen by 6.25; see Chapter 3, section 3.1.4) rose over the period 18 January to 25 May in a manner similar to that of gross foetal weight (Table 6.1; Figure 6.7). Estimated weight of protein was very highly correlated with increase in foetal weight ($r = 0.988$, $P < 0.01$; see Figure 6.8). It can be calculated that, over the whole of the assumed last two thirds of gestation, a gain in weight of 1.0 kg will have contained around 150g of protein.

6.2.5 INCREASE IN CHEMICAL FAT CONTENT.

The weight of chemical fat in the collected samples increased curvilinearly over the period of collection in the same manner as did gross foetal and foetal protein weights (Table 6.1; Figure 6.9). Thus fat is being deposited in the growing foetus at the same time that it is virtually completely disappearing from the body of the mother (see Chapters 3 and 5). It is of considerable interest that the weight of fat in the body of the foetus is very highly linearly correlated with gross foetal weight ($r = 0.981$, $P < 0.001$; see Figure 6.10). Thus, fat is being deposited in the foetus from the very earliest stages of development. Furthermore, the percentage of foetal weight that is fat also rises (albeit slightly; see Figure 6.11) over the gestation period.

6.3 Deposition of the major mineral nutrients.

6.3.1 DEPOSITION OF CALCIUM.

The percentage of calcium in the DM of the collected

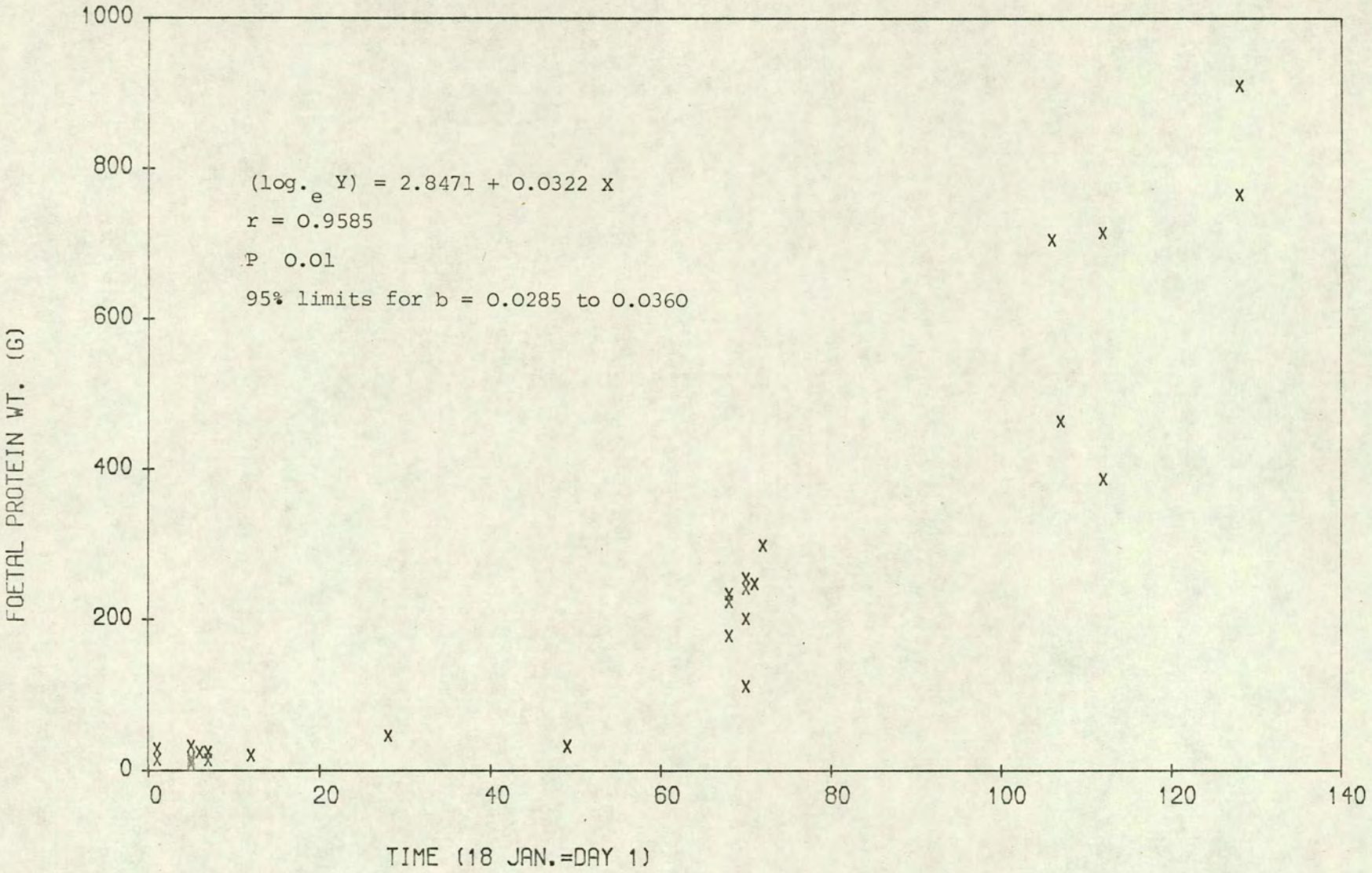

FIGURE 6.7. FOETAL PROTEIN VS. TIME

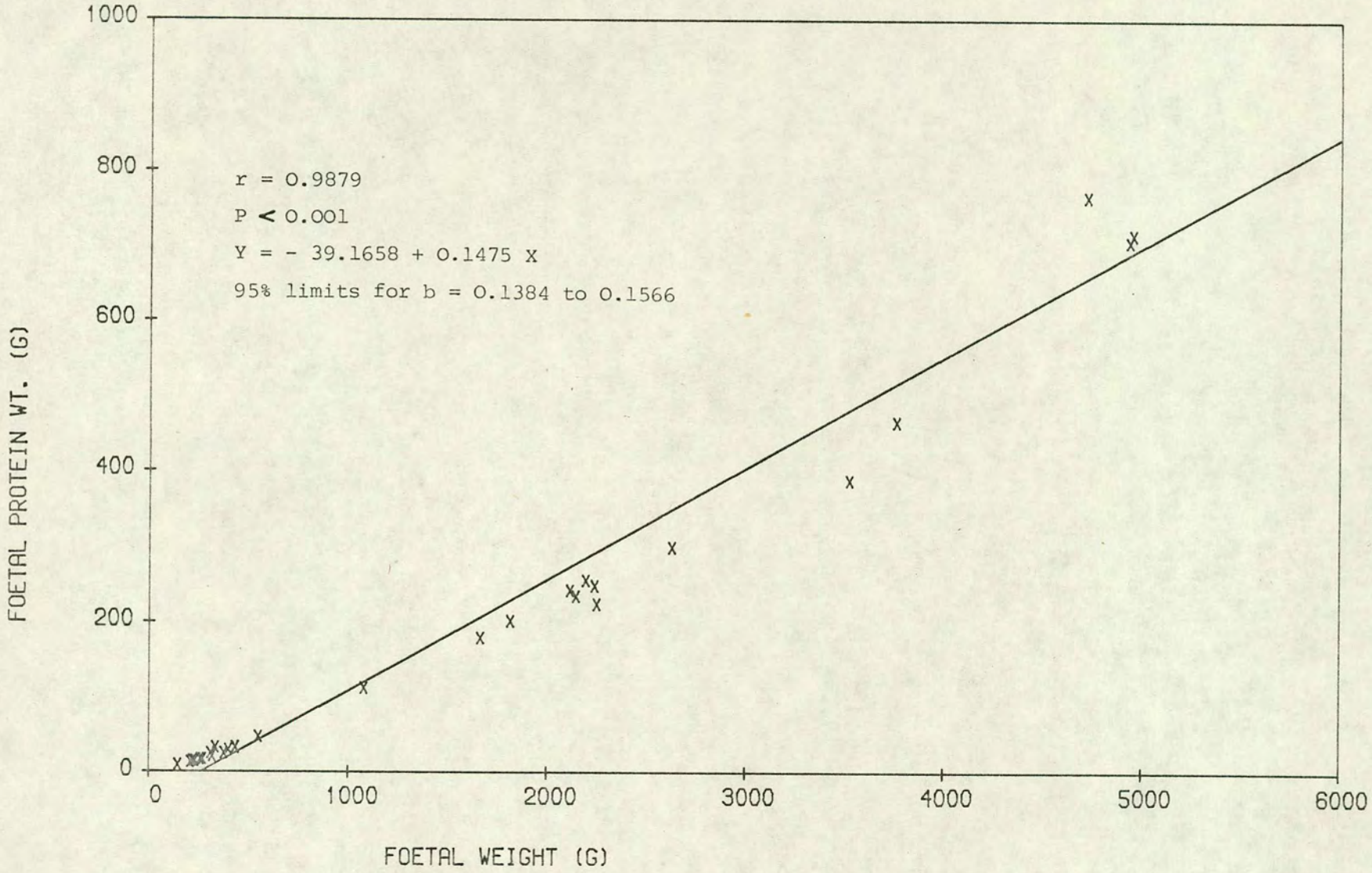

FIGURE 6.8: RISE IN PROTEIN VS. FOETAL WT.

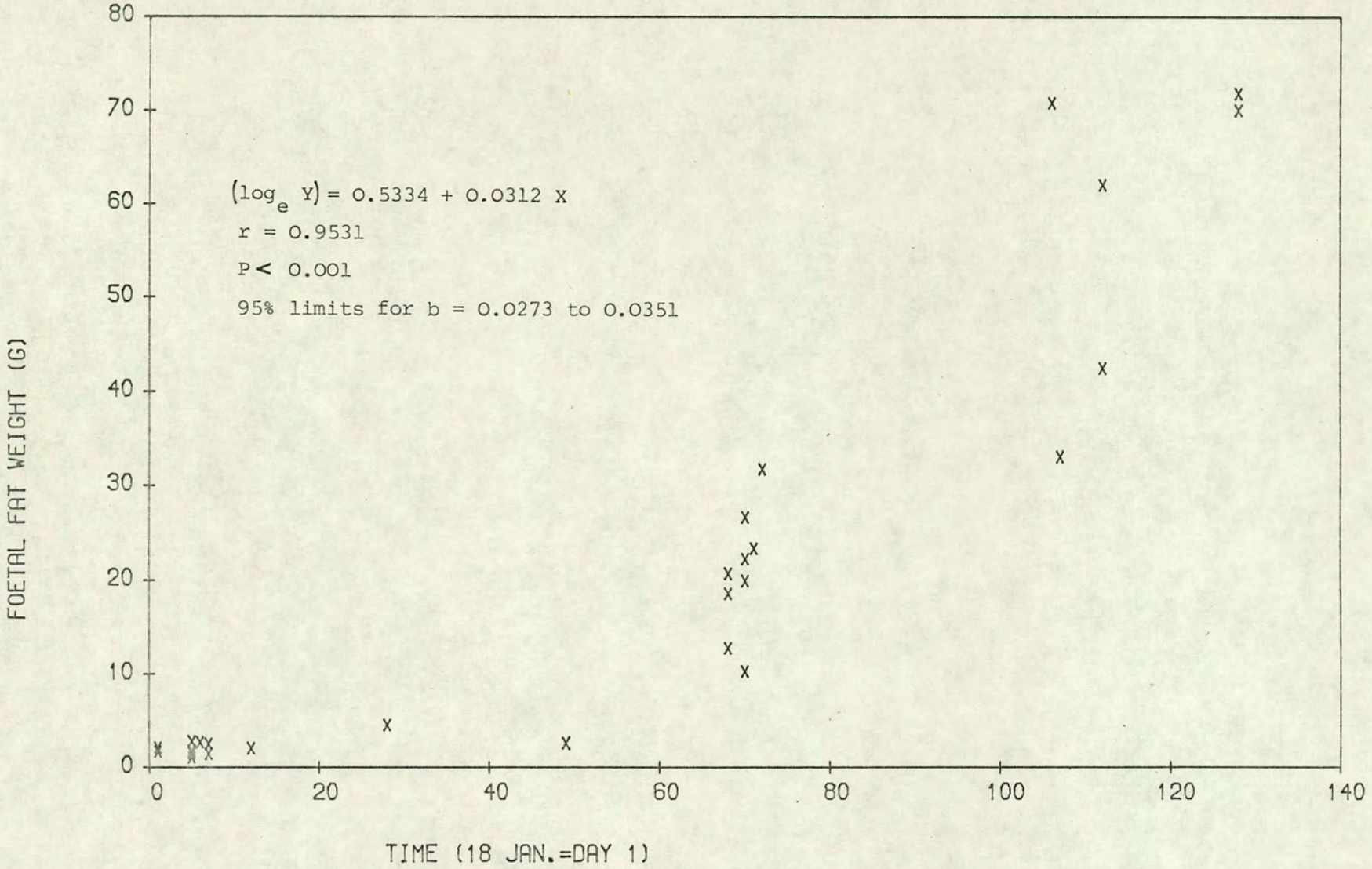

FIGURE 6.9. RISE IN FOETAL FAT VS. TIME

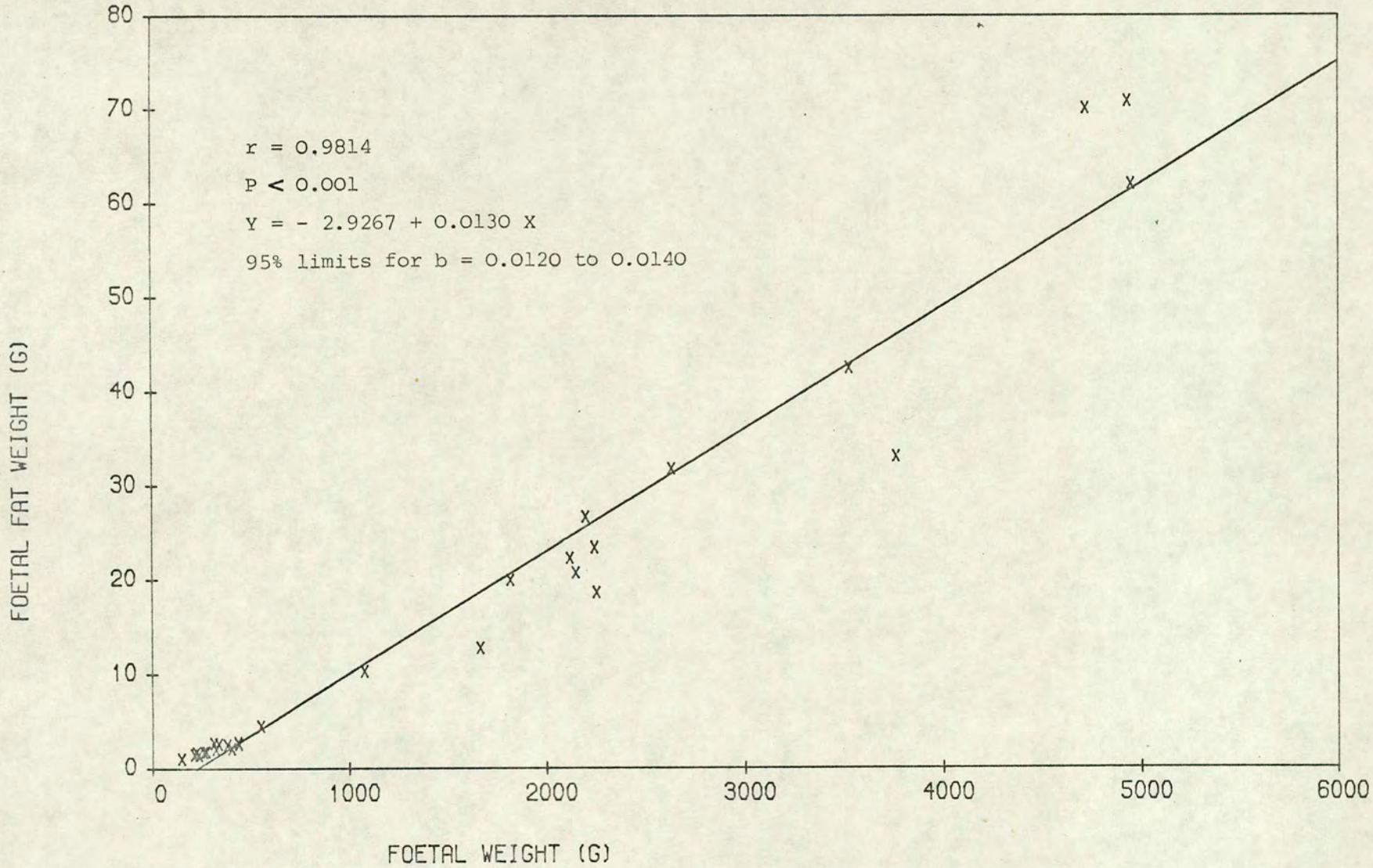

FIGURE 6.10. RISE IN FAT VS. FOETAL WT.

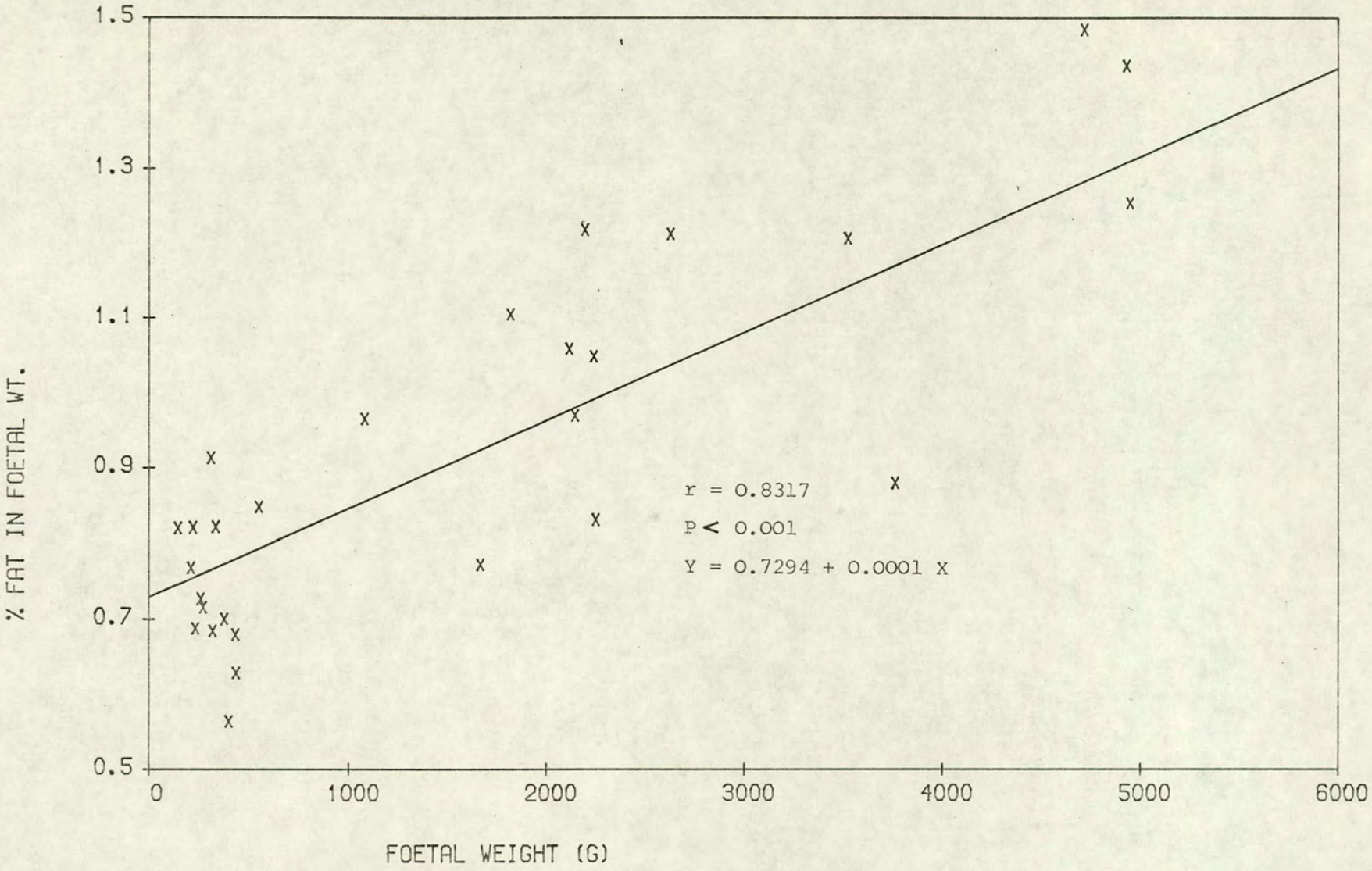

FIGURE 6.11. THE RISE IN % FOETAL FAT

foetuses showed no significant relationship with either the passage of time, or increase in foetal weight (Figure 6.12 and Table 6.2). Average DM content was 5.8% calcium, as compared to an average value of 5.3% in the DM of the samples representative of the empty bodies of the collected hinds (Chapter 3, section 3.1.5). It would appear that calcium has achieved its basic proportion in the DM of red deer from as early as the middle of the gestation period. As expected (since DM content of the foetus is increasing), the percentage of the whole foetal body that is calcium increases slightly (by around 0.1% per kg weight gain) as the foetus approaches term. Weight of calcium in the foetal body is very highly correlated with weight of the body itself ($r = 0.982$, $P < 0.001$), and a weight gain of 1 kg appears to contain about 13g of calcium. The estimated weights of calcium in the collected foetuses are shown in Figure 6.13. The rates of deposition of calcium in the foetuses are estimated by the two regression lines shown in the figure (the first derived from the data on foetuses 1 to 19, and the second from that on foetuses 20 to 35) as around 0.05g of calcium per day up until the middle of March, and around 0.84g per day thereafter.

6.3.2 DEPOSITION OF PHOSPHORUS.

The percentage of phosphorus in the DM of the collected foetuses, like calcium, was not significantly correlated with either the passage of time or the increase in gross foetal weight. Average % phosphorus in foetal DM was 3.4% (see Table 6.2), as compared to only 2.8% in the DM of the collected hinds, but both samples are too small for this to be taken as proof that a difference exists in the normal

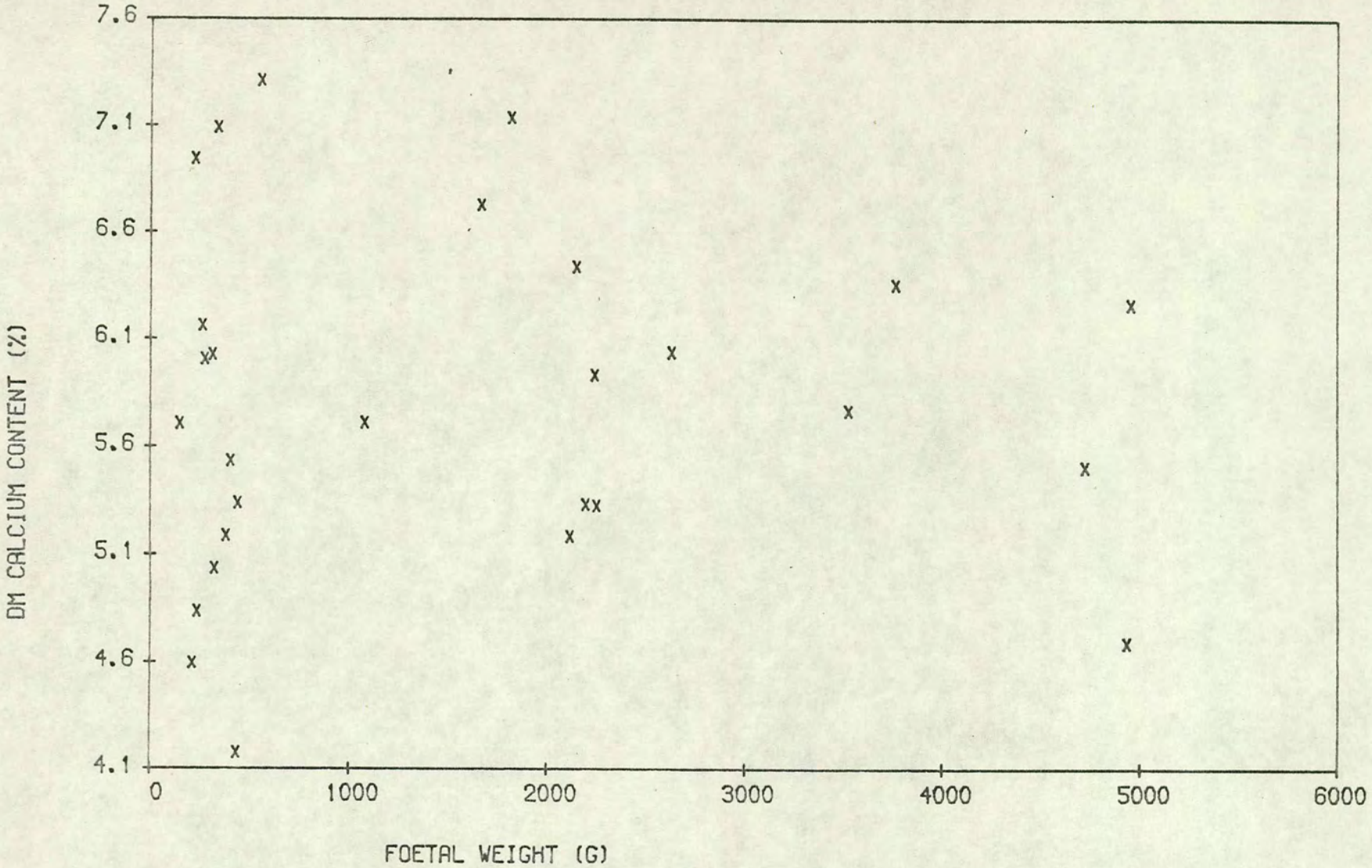

FIGURE 6.12.% CALCIUM IN FOETAL DM

FOETAL % CALCIUM	WEIGHT OF CALCIUM	FOETAL % PHOSPHORUS	WEIGHT OF PHOSPHORUS	FOETAL % MAGNESIUM
5.5400	3.0138	3.2240	1.7539	0.1670
6.9520	2.1259	3.9850	1.2186	0.1930
4.1810	2.3952	2.7820	1.5938	0.1610
6.0140	2.1265	3.4640	1.2249	0.1860
4.6030	1.2083	2.9290	0.7689	0.1280
6.1690	2.1493	3.6390	1.2678	0.1980
5.7140	1.1351	3.5470	0.7046	0.1700
6.0330	3.0020	3.5580	1.7705	0.1900
5.1940	2.5523	3.2490	1.5966	0.1830
4.8440	1.3935	3.1210	0.8978	0.1590
5.0440	2.0660	3.1500	1.2902	0.1560
7.3190	6.4810	4.0150	3.5553	0.2160
7.0980	4.1136	3.7840	2.1930	0.2150
5.3460	3.1933	3.1780	1.8983	0.1950
6.7350	20.2847	3.7710	11.3576	0.2050
6.4430	24.8764	3.4720	13.4054	0.1860
5.3350	19.6861	3.0710	11.3320	0.1640
5.7180	10.7254	3.3160	6.2199	0.1760
7.1440	24.2471	4.0020	13.5830	0.2060
5.3400	21.8016	3.1200	12.7380	0.1540
5.1900	19.5388	3.1140	11.7233	0.1560
5.9410	23.1556	3.5200	13.7195	0.1710
6.0460	29.2355	3.4010	16.4456	0.1580
4.6970	49.5844	2.6720	28.2073	0.1420
6.3610	50.2531	3.7050	29.2702	0.1720
5.7760	38.6738	3.0820	20.6358	0.1570
6.2670	67.6271	3.5730	38.5562	0.1600
6.5600	89.4216	3.4820	47.4643	0.1610
5.5110	59.3071	3.2400	34.8676	0.1410

30 GO :

Table 6.2.(a). The weights of the major mineral nutrients in th foetuses, and their percentages of the dry matter of the analysed samples. (see also Table 6.2.(b))

WEIGHT OF MAGNESIUM	FOETAL % SODIUM	WEIGHT OF SODIUM	FOETAL % POTASSIUM	WEIGHT OF POTASSIUM
0.0908	1.0790	0.5870	0.6420	0.3492
0.0590	1.3280	0.4061	0.9240	0.2826
0.0922	1.4790	0.8473	1.2380	0.7092
0.0658	1.5490	0.5477	1.0240	0.3621
0.0336	1.4320	0.3759	1.0050	0.2638
0.0690	1.5000	0.5226	1.0240	0.3568
0.0338	1.5440	0.3067	1.0870	0.2159
0.0945	1.3970	0.6951	0.9190	0.4573
0.0899	1.6140	0.7931	1.1230	0.5518
0.0457	1.4730	0.4238	1.0870	0.3127
0.0639	1.4810	0.6066	1.0620	0.4350
0.1913	1.2190	1.0794	1.1070	0.9802
0.1246	1.1020	0.6387	1.2550	0.7273
0.1165	1.5510	0.9264	1.3540	0.8088
0.6174	1.1880	3.5781	1.0500	3.1624
0.7181	1.0750	4.1506	0.9270	3.5791
0.6052	1.1490	4.2398	1.2940	4.7749
0.3301	1.4870	2.7892	1.2890	2.4178
0.6992	1.2580	4.2697	1.1370	3.8590
0.6287	1.1800	4.8176	1.0140	4.1399
0.5873	1.2510	4.7096	1.2840	4.8339
0.6665	1.2960	5.0513	1.1360	4.4277
0.7640	1.1920	5.7639	1.0130	4.8984
1.4990	0.8150	8.6036	0.7240	7.6430
1.3588	0.9240	7.2998	0.6750	5.3326
1.0512	0.8830	5.9122	0.6880	4.6066
1.7266	0.8090	8.7299	0.6340	6.8415
2.1946	0.8170	11.1368	0.6890	9.3920
1.5174	0.8310	8.9429	0.7000	7.5331

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Table 6.2.(b). Continuation of Table 6.2.(a).

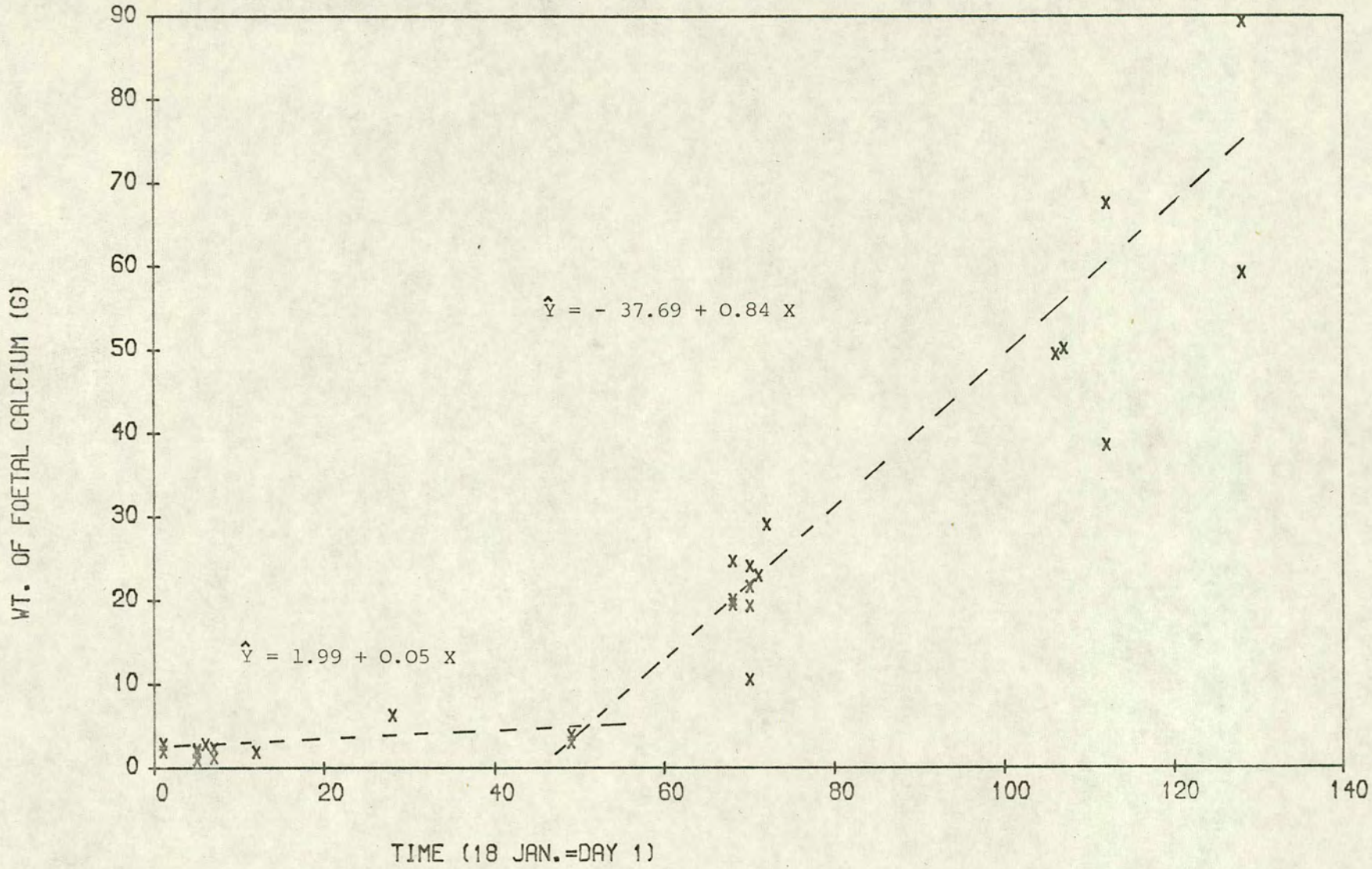

FIGURE 6.13. FOETAL CALCIUM DEPOSITION

levels of phosphorus in foetal as compared to adult deer. The increase in weight of phosphorus in the foetuses was highly correlated with the increase in foetal body weight ($r = 0.984$, $P < 0.001$), and was estimated to be occurring at a rate of around 7g of phosphorus per kg weight gain. Equations derived from the sampled foetuses estimate that phosphorus is deposited up until the middle of March at a rate of around 0.03g per day; after mid-March the deposition rate appears to be around 0.5g of phosphorus per day (Figure 6.14).

6.3.3 DEPOSITION OF MAGNESIUM.

Like calcium and phosphorus, the weight of magnesium in the foetuses appeared to be very highly correlated with the increase in gross foetal weight ($r = 0.992$, $P < 0.001$). Unlike these two major components of the skeleton, however, the percentage of magnesium in the DM of the samples significantly decreased as foetal weight increased (Figure 6.15). The weight of magnesium in the samples prior to mid-March was so low as to be nearly negligible (Table 6.2); after the middle of that month it is estimated to have been deposited at a rate of around 0.013g per day (or around 0.3g per kg foetal weight gain).

6.3.4 DEPOSITION OF SODIUM.

Like magnesium, the percentage of sodium in the foetal DM decreased as foetal body weight increased ($r = -0.866$, $P < 0.001$; Figure 6.17). Weight of sodium in the foetuses was linearly related to foetal body weight ($r = 0.992$, $P < 0.001$), and a foetal weight gain of 1 kg contained an estimated 1.8g of sodium. Unlike the curvilinear increase in the weights of

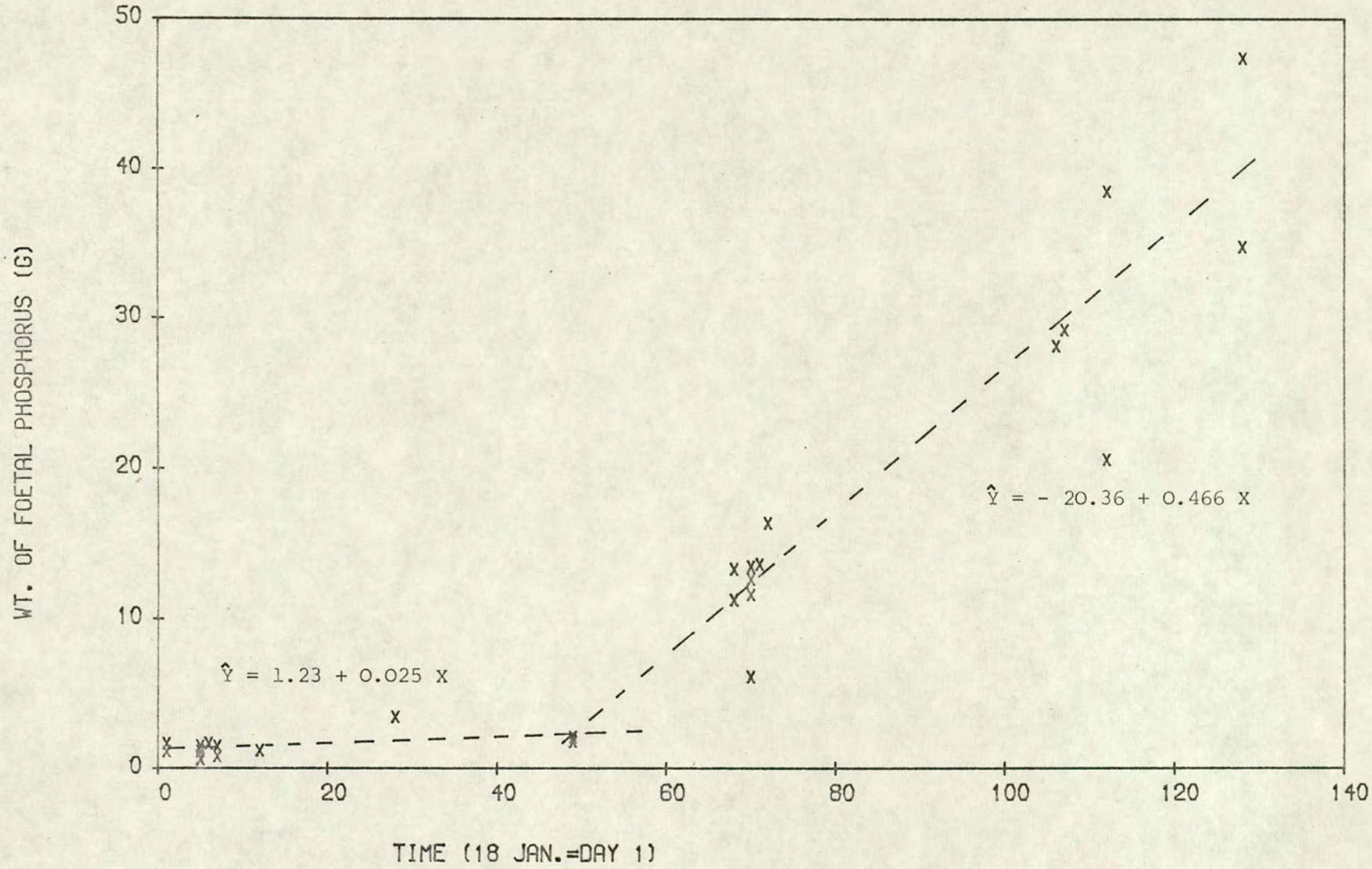

FIGURE 6.14. DEPOSITION OF PHOSPHORUS

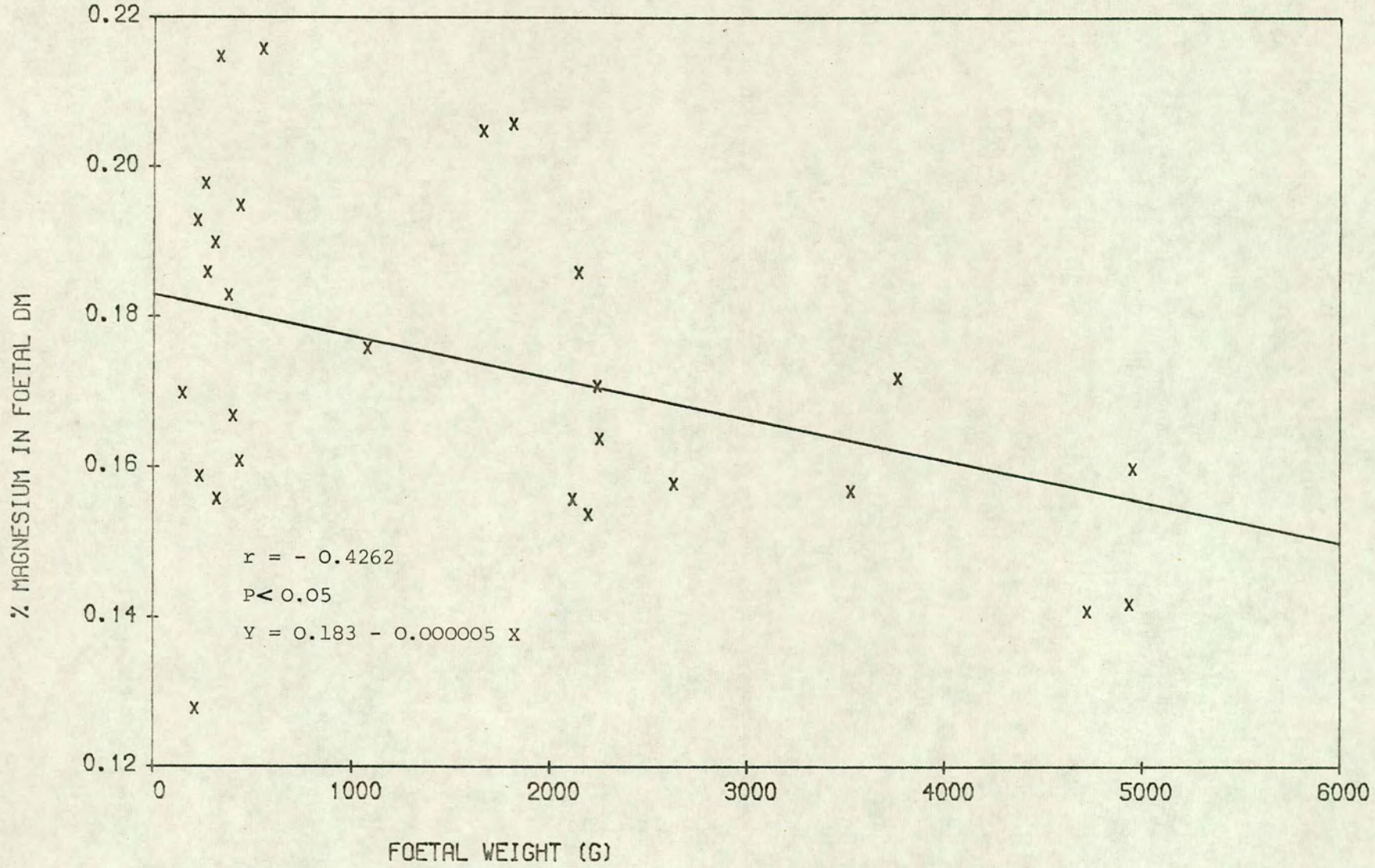

FIGURE 6.15. DECREASE IN % MAGNESIUM IN DM

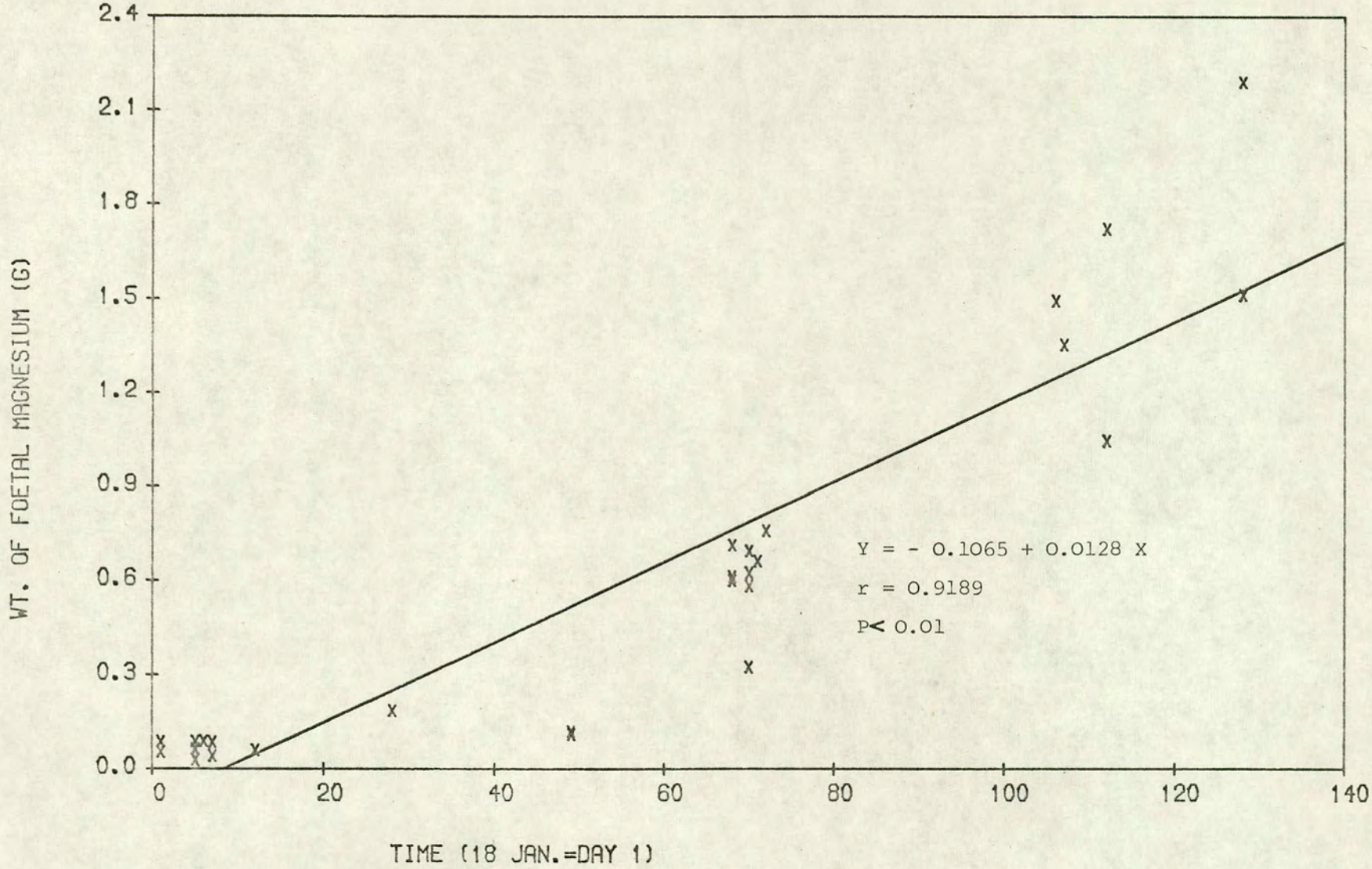

FIGURE 6.16. DEPOSITION OF MAGNESIUM

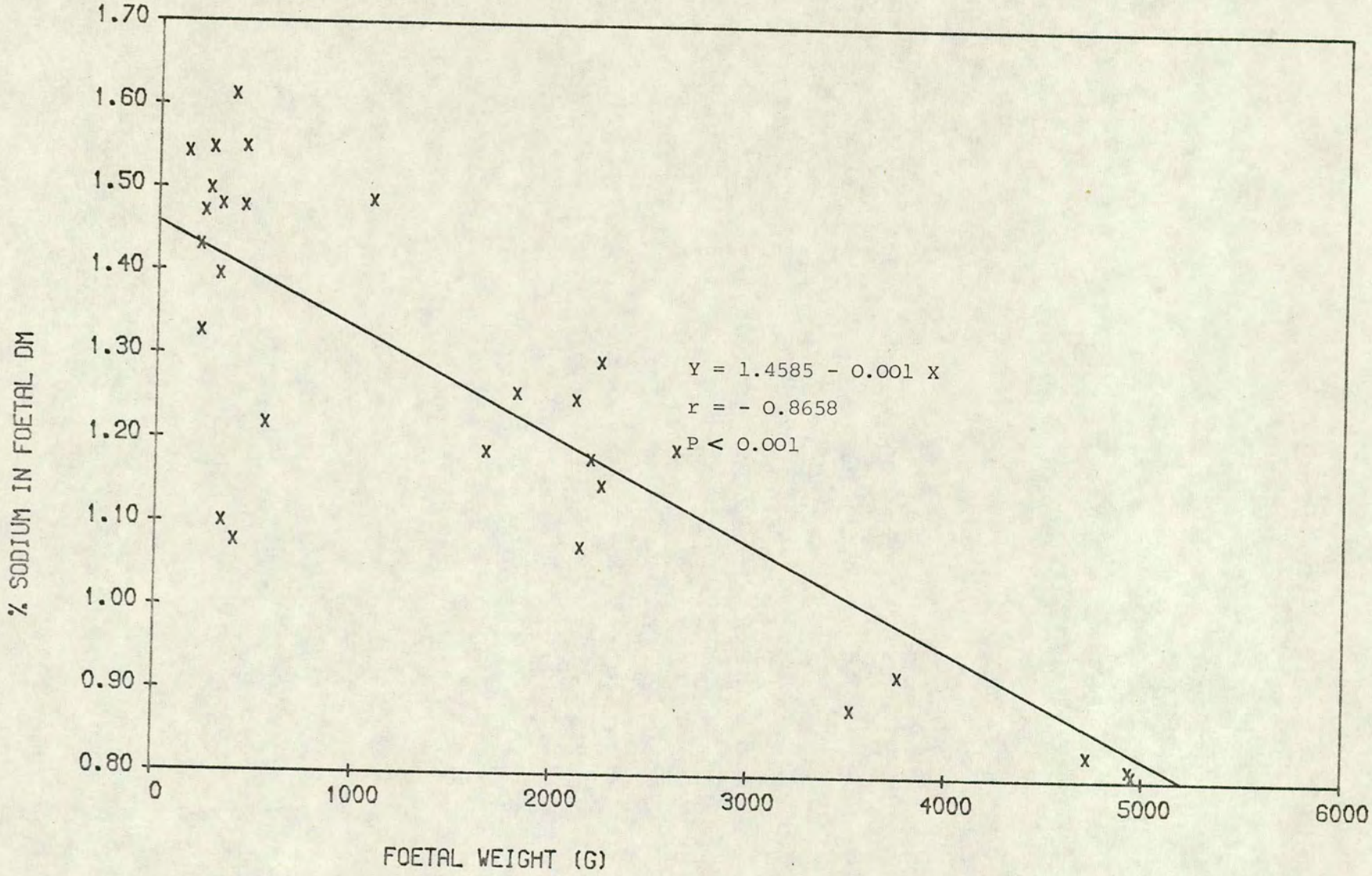

FIGURE 6.17. DECREASE IN % SODIUM IN DM

calcium or phosphorus, the weights of sodium in the collected foetuses appeared to be better estimated by a single linear regression, increasing at an estimated rate of around 0.07g of sodium per day over the whole period 18 January to 25 May (Figure 6.18).

6.3.5 DEPOSITION OF POTASSIUM.

The percentage of potassium in the DM of the foetuses initially decreased as foetal weight increased, but appeared to have reached a relatively constant level (of around 0.7% of the DM) by the time a foetus reached around 3 kg in size (Table 6.2 and Figure 6.19). This value is slightly lower than the 0.8% found in the DM of the adult hinds; again, the samples are too small for this to be accepted as evidence of a difference between levels of potassium existing between foetal and adult deer. Like all the other major minerals, weight of potassium in the foetuses was highly linearly correlated with foetal body weight ($r = 0.978$, $P < 0.001$), and a foetal weight gain of 1 kg is estimated to have contained around 1.5g of potassium. Like sodium, the increase in the weight of potassium in the foetuses was well described by a simple linear equation (Figure 6.20), and is estimated to have been accumulating in the foetal body at a rate of around 0.06g per day over the whole of the period of collection.

6.4 Comparison of foetal compositional development in red deer and white-tailed deer.

Robbins and Moen recently (1975) have reported on the composition of the uterus and its contents during foetal development of the white-tailed deer. A variety of differences

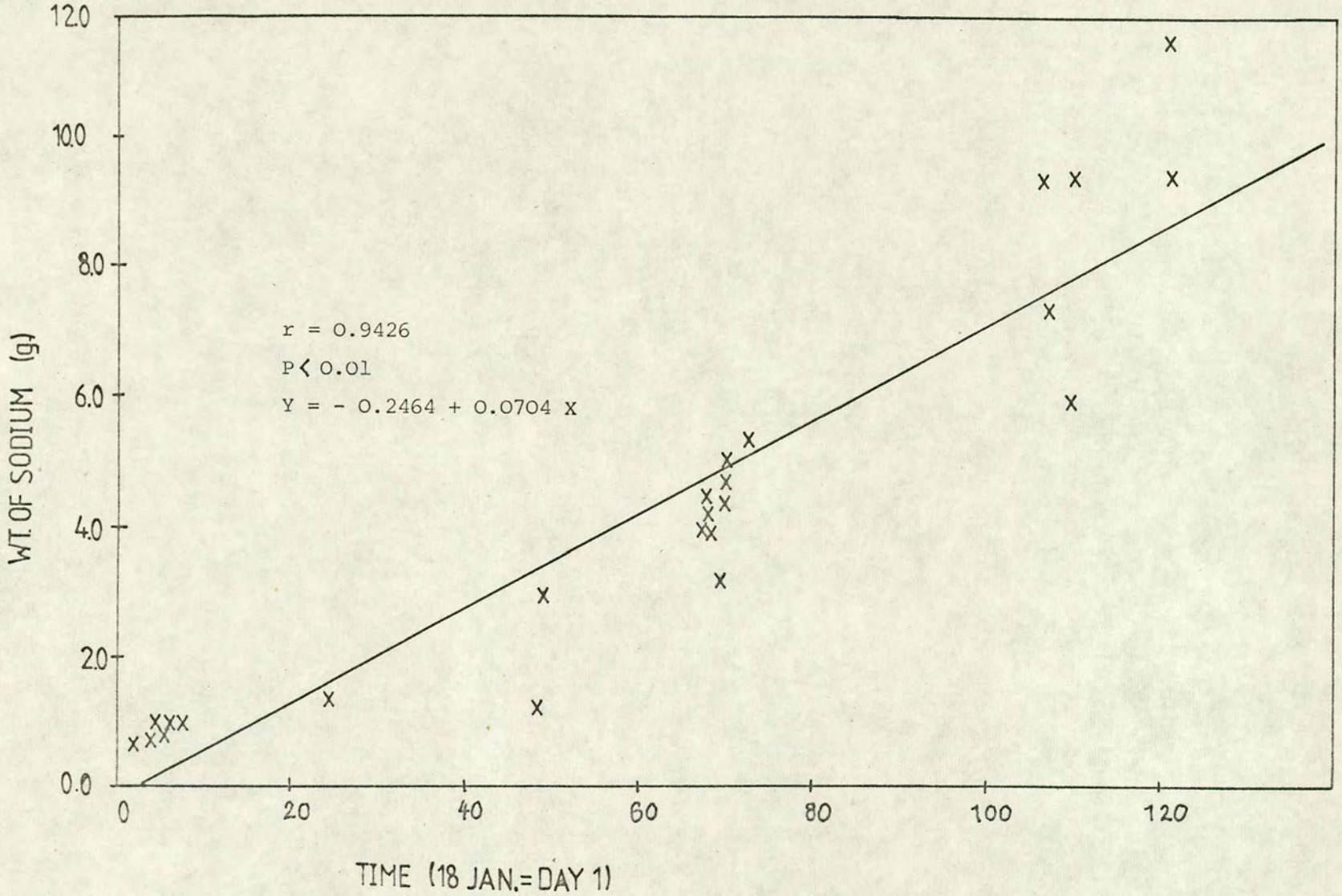

FIGURE 6.18. DEPOSITION OF SODIUM

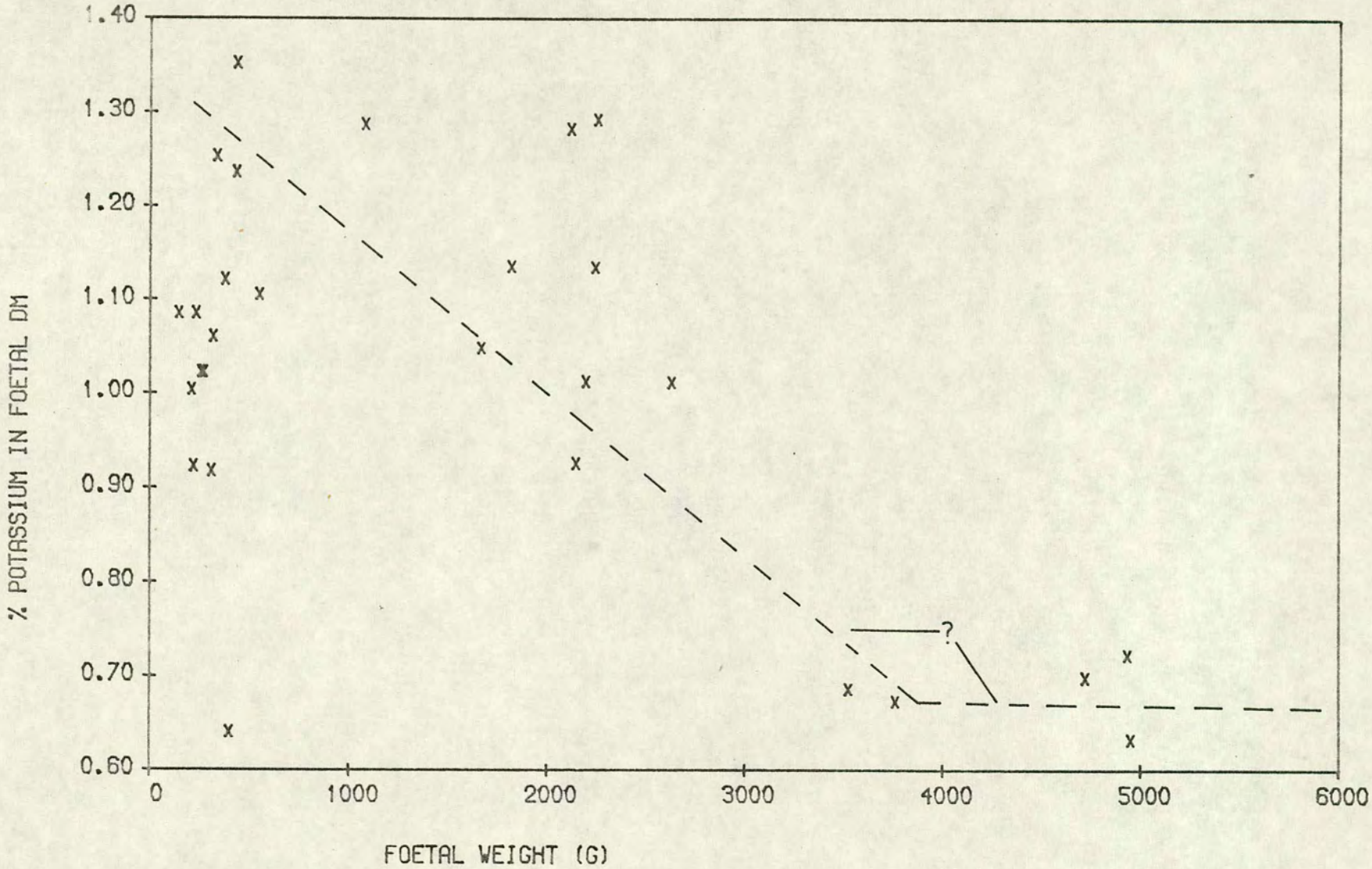

FIGURE 6.19. DROP IN % POTASSIUM IN DM

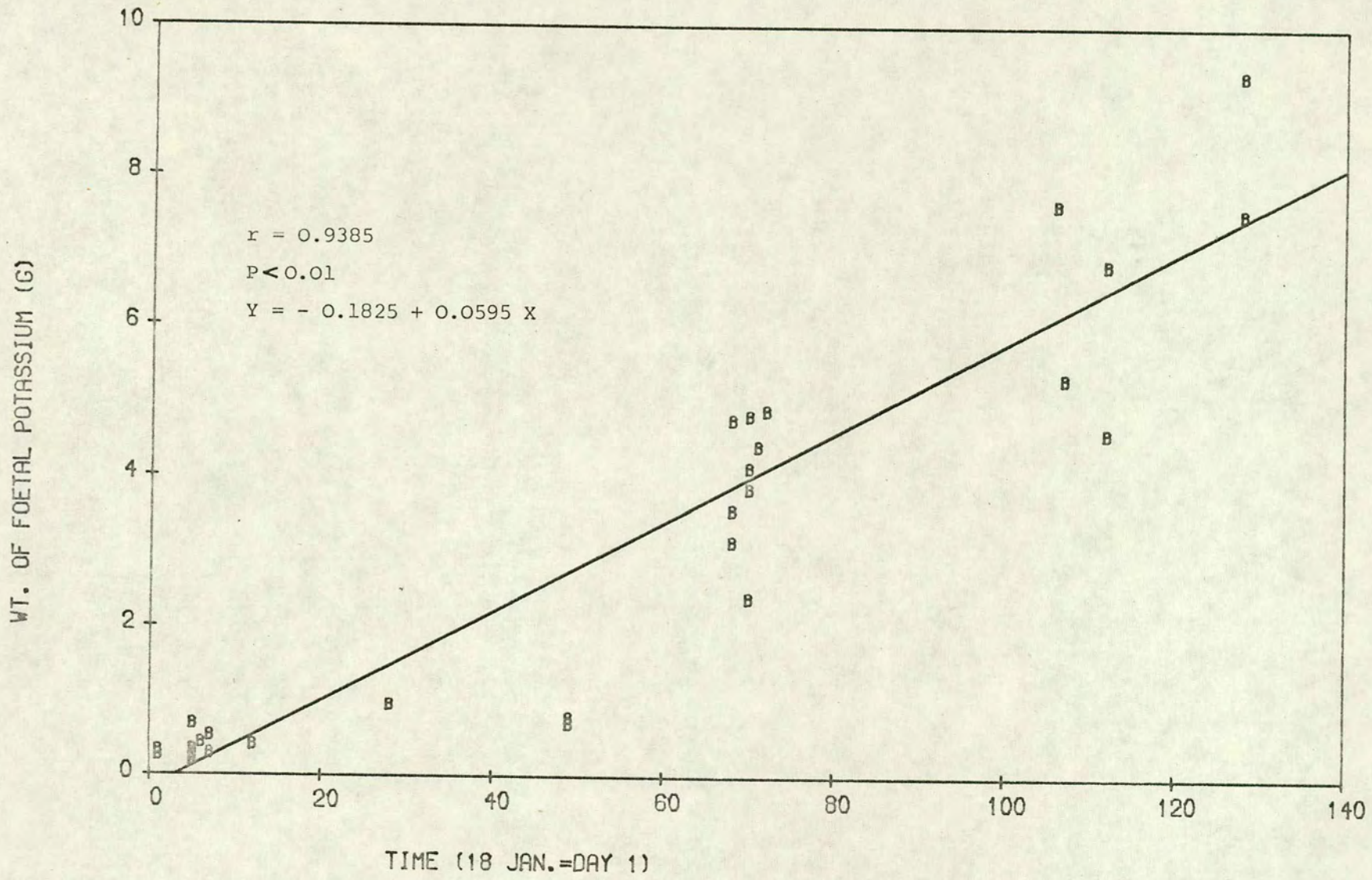

FIGURE 6.20. DEPOSITION OF POTASSIUM

exist between red and white-tailed deer, both reproductively, and in general features: for example, white-tailed deer often bear twins or even triplets, while twinning in red deer appears to be exceedingly rare (see Chapter 1, section 1.4). White-tailed deer also tend to be smaller at birth than red deer: the average birth weight of white-tailed deer reported by Robbins and Moen from a variety of sources was 3.12 kg; the average reported by Mitchell (1971B) for Scottish red deer was 6.57 kg. White-tailed deer also have a shorter average gestation period (perhaps because of their smaller size), of only around 200 days (Severinghaus and Cheatum, 1952; in Robbins and Moen, 1975), as compared to the average of around 233 days found by Guinness et al (1971) in their study of red deer hinds on the Isle of Rhum.

In view of the differences just mentioned, the very similar composition of red and white-tailed deer foetuses, even at equivalent stages of development, may be thought quite surprising. Because of the difference in gestation length, I have estimated the ages of the red deer foetuses as explained in the table, and the comparisons thus are made at (assumed) equivalent stages of development. It is particularly striking that, even although the ages of the red deer foetuses are only rough estimates, the water, nitrogen, fat and energy contents of the foetuses of the two species are virtually identical (Table 6.3).

Robbins and Moen propose in their paper (p.688) that, at equivalent stages of development (% of gestation elapsed), the energy contents of the gravid uteruses (divided by average weight, in kg., at birth) are very similar in white-

Table 6.3 Composition of red deer and white-tailed deer foetuses at (estimated) equivalent stages of development.*

Species	Number of foetuses	Proportion of gestation elapsed	Weight (kg)	H_2O (%)	Nitrogen (%)	Fat (%)	Energy content (kcal/kg)
white-tailed deer	4	0.50 (100 days)	0.289	88	1.28	0.72	539.78
red deer	1	0.50 (116 days)	0.550	84	1.41	0.85	697.55
white-tailed	4	0.72 (145 days)	1.259	82	1.85	1.18	843.24
red	9	0.72 (168 days)	2.020	82	1.78	1.03	807.50
white-tailed	4	0.95 (190 days)	3.574	78	2.35	2.16	1033.32
red	2	0.95 (221 days)	5.362	77	2.54	1.36	1033.76

*Data on white-tailed deer calculated from Robbins and Moen (1975). That on red deer from present study.

All figures are averaged values.

Age of red deer foetuses estimated by assuming conception on 19 October.

tailed deer, cattle and sheep. In view of the close similarity in foetal energy content shown in Table 6.3 between red deer and white-tailed deer, it appears justifiable to assume that the energy content of the gravid uterus of red deer at any particular point during gestation may be estimated accurately by the formula derived by Robbins and Moen from data on cattle, sheep and white-tailed deer:

natural log Y = 2.1548 + 0.0501 X;

where Y = the energy content of the whole gravid uterus in kcal, divided by average foetal birth weight (kg), and
X = stage of gestation (expressed as a percentage).

6.5 Summary of the compositional development of the collected foetuses.

6.5.1 GROWTH AND COMPOSITION OF THE FOETUSES.

The weights of the collected foetuses were found to be well related to the passage of time by a simple linear regression on the cube root of foetal weight, similar to many other mammalian species (Huggett and Widdas, 1951). The rate of increase in foetal weight was found to be low until around the middle of February, after which it rose in exponential style. The weight of foetal DM was found to increase in a manner similar to overall foetal body weight. Foetal DM formed an increasing percentage of foetal body weight as that weight increased, although it appeared that the rate of increase in percent DM began to decrease over the final third of the gestation period. Foetal gross energy content also increased curvilinearly over the period 18 January to 25 May: the rate of gain was estimated to have been around 8.8 kcal per day until around the 15th of March, after which it was estimated at around 64.1 kcal per day.

Gross energy content, and weights of DM, protein and fat were all found to be highly linearly correlated with the increase in foetal body weight. Interestingly, chemical fat was found to be increasing linearly with the increase in body weight from the earliest stage of development examined. Thus growth, even in the foetus, is not exclusively an increase in muscle and bone tissue; the growth of fatty tissue (or at least the deposition of chemical fat) appears equally to be an integral part of the growing process.

The weights of all the major mineral nutrients were highly linearly related to the increase in gross foetal weight. The weights of calcium and phosphorus in the foetus sample increased curvilinearly over the period 18 January to 25 May, and their percent contributions to DM weight did not change, either with the passage of time or the growth in weight of the foetus. Magnesium, sodium and potassium appeared to increase more or less linearly over the collection period, while the percentages of all three in the DM of the foetuses decreased as foetal body weight increased. The reason for this presumably is the increasing contribution of nitrogen (largely in protein) and chemical fat to the weight of the DM as the foetus approaches term.

The increase in energy content and the deposition of minerals in the developing foetus are discussed further in the next chapter, in relation to the energy and nutrient costs of pregnancy to wild red deer.

6.5.2 COMPARATIVE DEVELOPMENT OF THE FOETUS IN RED DEER AND WHITE-TAILED DEER.

By estimating the ages of the red deer foetuses, comparison has been made between the water, nitrogen, fat and energy contents of foetal red deer and foetal white-tailed deer. At estimated equivalent stages of gestation, the composition of the foetuses of the two species have been found to be virtually identical.

In conclusion, it appears that the energy content of the gravid uterus of red deer, at any given stage of gestation, can be estimated by a formula derived from white-tailed deer. Furthermore, in view of the apparent close similarity in foetal composition of cattle, sheep and white-tailed deer (when differences in gestation length and birth weight are accounted for), it appears justifiable to assume that relationships derived from data on these species also are applicable to foetal development in red deer. It was to be borne in mind, however, that the above assumption is based on the apparent similarities in energy content and composition of the uterus and its contents. Estimates of the pregnancy requirements of cattle and sheep which have been derived by other methods may include partial requirements for maternal tissue changes which are not similar to those of pregnant red deer hinds.

CHAPTER 7. The Energy Requirements of Wild Hinds for Winter Weight Maintenance and Pregnancy.

In Chapter 1 I expressed the intention to carry out research to make possible the calculation of the amounts of energy daily required by wild hinds, over the whole of the winter:

(i) to maintain approximately constant body weight; and

(ii) the energy and other nutrients additionally required for the reproductive process.

In this chapter the energy dynamics of the bodies of the hinds and of the foetuses (as indicated by the information presented in the previous chapters) are summarised. Because of the curtailment of the collection period, estimates are applicable only to it. The problems posed by energetic efficiencies to attempting to use this information to achieve the stated intentions, and the conclusion that estimates of requirements are dependent on assumptions made about efficiencies of energy use, are briefly presented and discussed. Such assumptions then are made and estimates of the requirements for pregnancy and winter weight maintenance are presented. It is emphasised that the accuracy of these estimates cannot be assessed at present.

7.1 Energy dynamics of the hinds and foetuses.

7.1.1 RATE OF ENERGY LOSS BY THE HINDS.

As shown in Chapter 3 (and discussed in Chapter 5), the 19 hinds examined in this study were losing energy from their bodies (not including the contents of the conceptus) at an average rate of 561 kcal per day over the period 14 February to 25 May. The body weights of the hinds were also decreasing over this period, and it has

been argued (Chapter 5) that this loss occurred because the hinds were experiencing an energy deficit (evidenced by their need to expend body sources of energy). From the relationship between the weight of a hind's empty body and her gross energy content (see Figure 5.9), it appears that a loss of 1 kg of empty-body weight was accompanied by a loss of around 3.74 Mcal of body energy. Various equations describing the rate at which energy loss occurred are given in Table 7.1.

Table 7.1 Estimated rates of loss of empty-body gross energy content (X = no. of days since 14 February; Y = as shown):

Regression	Correlation coefficient	Description of body energy content
$Y = 124.950 - 0.5611\ X$	$r = -0.836$ (P 0.01)	Y = empty-body gross energy (Mcal)
$Y = 1.7968 - 0.0073\ X$	$r = -0.895$ (P 0.01)	Y = Mcal/kg of live weight
$Y = 2.4206 - 0.0083\ X$	$r = -0.884$ (P 0.01)	Y = Mcal/kg empty-body weight
$Y = 6.4890 - 0.0241\ X$	$r = -0.884$ (P 0.01 0	Y = Mcal/kg 'metabolic' empty-body weight. (empty-body weight$^{0.75}$)

The rate at which hinds lose energy will vary between animals (due to differences in metabolic rates and in the amounts of energy expended in muscular activity, lactation and pregnancy); between areas (depending on differences in the environmental demand made by weather; the amounts of shelter available that can be used to escape from or reduce this demand; and the amounts of dietary energy available from the vegetation); and even between years in the same area, (again, depending on the weather and its effects on

environmental demand and vegetative energy supply). However, the hind sample contained animals from the full range of 'adult' age classes (4 to 10 years), all of which were pregnant, and which had been collected from a variety of areas, during what was probably an 'average' winter (1973). It therefore appears legitimate to assume that the rate of daily energy loss derived from them is fairly typical of the amounts of energy lost by pregnant hinds, in many parts of the Highlands, over the period mid-February to the end of May (for a fuller discussion of the representativeness of the hind sample, see Chapter 2, section 2.8).

Although the hinds of this study were having to expend body energy at a rate of around 0.561 Mcal/day, not all of this energy was actually lost from their bodies. Until now the bodies of the hinds have been examined excluding the contents of the gravid uteruses. This has been done so that the energy dynamics of the hinds could be investigated in isolation, in the hope that the amount of energy required for body maintenance could be calculated separately from the amount required by the products of conception (it was for that reason that the uteruses and mammary glands - as parts of the hinds - were analysed with the offal components of the bodies). The ability to achieve the above goal (i.e., to calculate maintenance, separately from pregnancy, requirements) is discussed in section 7.3.3. of the present chapter.

7.1.2 ENERGY DEPOSITED IN THE GRAVID UTERUS.

Although the energy content of the conceptuses of the hinds is not known (since the energy content of the uterus

and its fluids, and of the foetal membranes, were not determined separately), it appears that the energy in the whole gravid uteruses can be reasonably estimated by the equation of Robbins and Moen (1975); provided that foetal age can be accurately estimated, and a figure for average birth weight is available which resembles that which would have been achieved by the collected foetuses. The ages of the foetuses therefore have been estimated, using the model of Mitchell and Lincoln (1973). The legitimacy of doing so depends upon the correctness of the assumptions upon which the model is based: that the mean gestation length of Scottish red deer is close to 233 days; mean birth rate is near to 6.57 kg; and that the X-intercept of the estimating equation of the modeliis near 0.146 in value (Mitchell and Lincoln obtained this value from data on North American elk, Cervus elaphus canadensis). The legitimacy of the model is also dependent on the correctness of the assumption that foetal weight is (almost) entirely a function of foetal age. The figure of 233 days appears to have become generally accepted as an average value for gestation length in Scottish red deer, while the value of 6.57 kg for mean birth weight is based on what seems to be a sufficiently large sample (236 calves; Mitchell, 1971b). Since elk are larger than Scottish red deer, the value of 0.146 (for the X-intercept of Mitchell and Lincoln's model) may be somewhat low (i.e., being smaller, red deer foetuses may take slightly longer before the cube root of weight rises measurably above zero). However, since foetal development seems to be remarkably similar in a wide variety of ruminant species, if there be a difference between the assumed value and the real one for red deer, it seems reasonable to expect it to be small enough

so as not to invalidate the use of Mitchell and Lincoln's model. The assumption that foetal weight is entirely a function of age is not strictly correct. It has been shown both in cattle (e.g., Tudor, 1972), and more recently in North American elk (Thorne et al, 1976), that poor maternal nutrition, especially during the last third of gestation, leading to body weight losses in the dam, can significantly reduce birth weight of the offspring. The model of Mitchell and Lincoln (1973) therefore may underestimate age (based on foetal weight) of some foetuses during the final third of the development period. However, a decrease in foetal growth rate, due to poor maternal nutrition during the final stages of pregnancy, presumably will be accompanied by a decrease in growth rate of the whole of the gravid uterus (the energy content of which is being estimated here from foetal age). In any case, the hinds of the present study probably were subjected to similar levels of undernutrition, so that a similar level of error will have been applied to them all.

The energy contents of the gravid uteruses of the collected hinds (as estimated from the equation of Robbins and Moen, 1975, having first estimated the age of the foetuses by the model of Mitchell and Lincoln, 1973) are shown in Table 7.2. The table also shows the estimated gross energy content of the live hinds when the energy in the gravid uterus is included (but excluding the energy contained in the gastro-intestinal tract). The difference between the determined energy contents of the empty bodies of the hinds and the estimated content of the whole hind plus foetus (less some blood loss) is shown in Figure 7.1. It can be seen from

FOETUS SAMPLE NUMBER	FOETAL ENERGY (KCAL)	CONCEPTUS ESTIMATED GE (KCAL)	% OF UTERINE GE IN FOETUS
1.0000	241.8700	633.5344	38.1779
2.0000	124.3500	467.4407	26.6023
3.0000	261.2200	663.6143	39.3632
4.0000	152.6200	517.1404	29.5123
5.0000	117.0600	457.6292	25.5797
6.0000	152.5000	505.8430	30.1477
7.0000	81.7800	390.8760	20.9222
8.0000	219.2600	553.3025	39.6275
9.0000	215.7900	613.9294	35.1490
10.0000	130.3900	479.0952	27.2159
12.0000	183.1500	561.5437	32.6154
17.0000	383.6499	764.9160	50.1558
18.0000	248.9700	575.2053	43.2837
19.0000	267.1599	665.3772	40.1516
20.0000	1340.7500	1763.2139	76.0401
21.0000	1771.9700	2239.2998	79.1305
22.0000	1666.0698	2347.7434	70.9647
23.0000	816.7100	1224.5146	66.6966
24.0000	1461.8799	1909.1125	76.5738
25.0000	1872.4500	2290.7275	81.7404
26.0000	1741.5098	2208.6121	78.8509
27.0000	1743.4700	2337.3430	74.5919
29.0000	2162.6299	2752.3052	78.5752
30.0000	5194.2773	5746.0039	90.3981
31.0000	3422.1899	4107.1758	83.3222
32.0000	3062.5698	3804.5493	80.4976
33.0000	4741.4570	5771.7031	82.1500
34.0000	6039.5078	7477.2188	80.7721
35.0000	4905.7773	5428.8594	90.3648

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Table 7.2. Gross energy content of the foetuses, the energy content of the whole gravid uterus (estimated by the equation of Robbins and Moen, 1975), and the percentage of the energy of the gravid uterus contained within the foetus, over approximately the last two-thirds of gestation (18 January to 25 May).

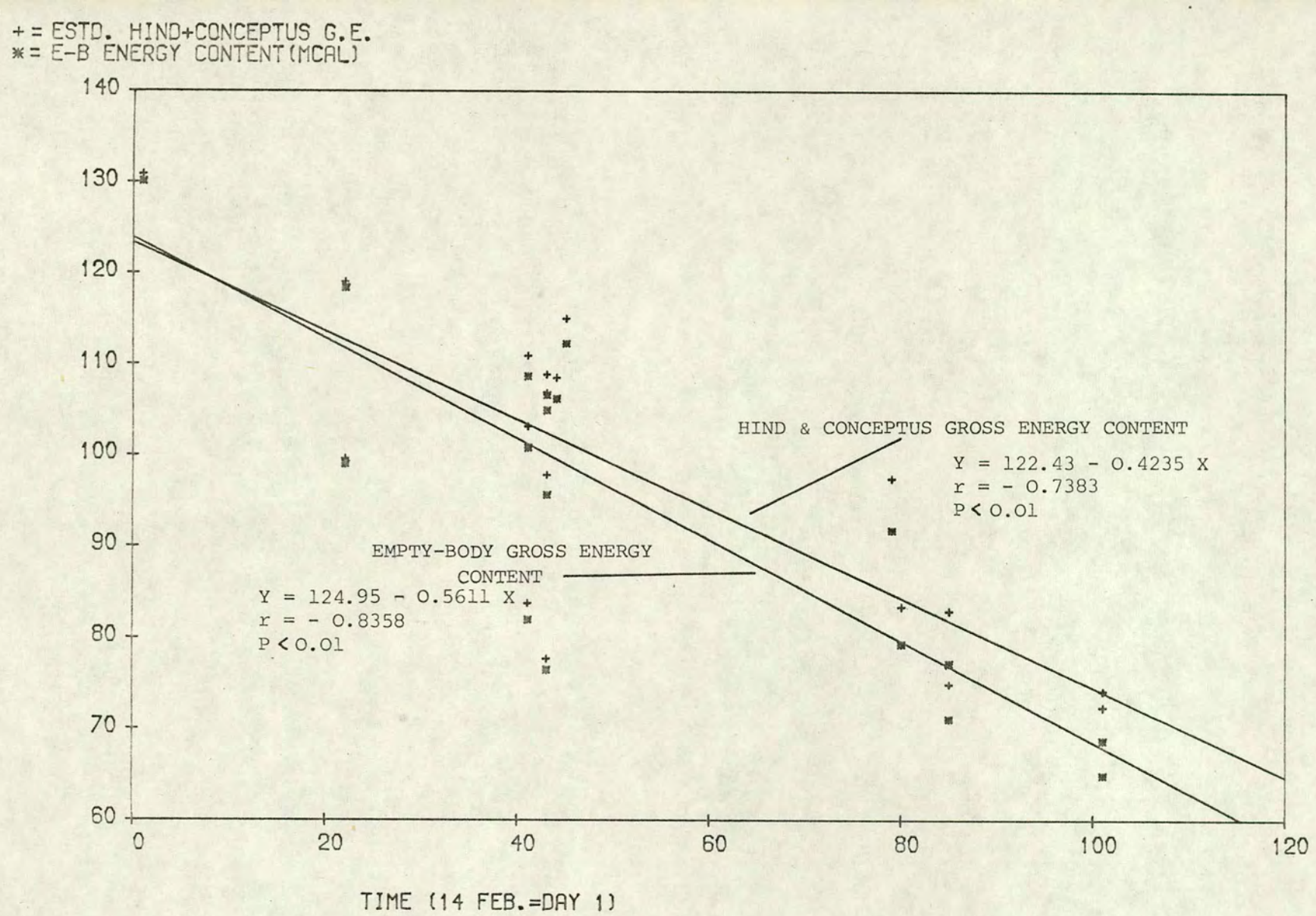

FIGURE 7.1 EMPTY-BODY VS HIND+CONCEPTUS G.E. LOSS

the figure that although the hinds were found to be losing energy to the extent of 0.561 Mcal/day over the collection period, the estimate of actual loss from the whole of the body is 0.49 Mcal/day (due to the deposition of some energy in the gravid uterus). The energy content of the gravid uteruses, as estimated by the equation of Robbins and Moen, increased over the period when foetuses were collected (18 January to 25 May) as shown in Figure 7.2. It can be seen from the figure that the energy contained in the whole of the conceptus appears to increase in the same curvilinear manner as was determined for the energy contents of the foetuses themselves. Thus, energy appears to be deposited in the conceptus, up until the middle of March, at a rate of only 3.0 kcal/day; after mid-March the rate of deposition is estimated to be around 0.072 Mcal/day.

7.1.3 SUMMARY OF THE ENERGY DYNAMICS OF THE HINDS AND FOETUSES.

Over the 100-day period during which hinds were collected (14 February to 25 May) empty-body gross energy content dropped at an average rate of 0.561 Mcal (or 8.3 kcal/kg of empty-body weight) per day.

Over the period during which foetuses were collected (18 January to 25 May) foetal gross energy content was found to rise from around 0.18 Mcal to around 5.0Mcal. The estimated rate of deposition of energy in the whole gravid uterus over the period 18 January to 15 March was 0.003 Mcal/day. After the 15th of March the rate of deposition is estimated to have been 0.072 Mcal/day. Confidence in the accuracy of this estimate (0.072 Mcal, or 71.7 kcal/day) is gained from its comparison with data of Rattray et al (1974); who

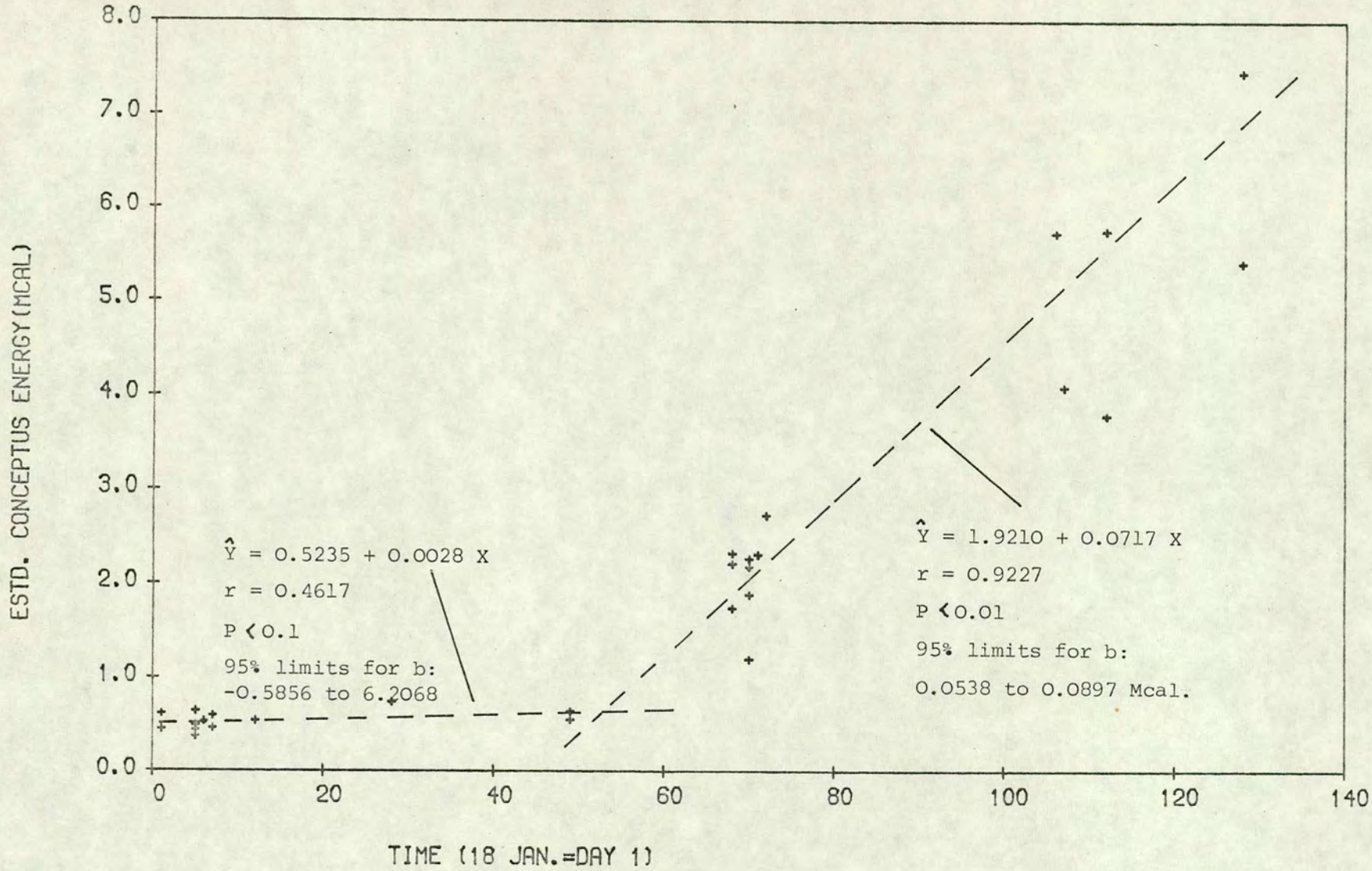

FIGURE 7.2 ESTD. RISE IN CONCEPTUS ENERGY

found that energy was stored in the conceptus of sheep, over the final 100 days of gestation, at rates of from 66 kcal/day (sheep on 'low' level of nutrition; i.e., 1.5 X's maintenance) to 79 kcal/day (sheep on 'high' level of nutrition; i.e. 2.0 X's maintenance).

7.2 The problem of energetic efficiences.

Since the bodies of red deer (and all other animals) contain energy it is possible to view them as energy stores. Body energy is in a state of constant flux, however, the dynamics of which can be described by the simple model:

$$dE/dT = E_{intake} + E_{output};$$

where dE/dT is the change in body gross energy content per unit time, E_{intake} is the amount of energy absorbed by the animal's body over that time, and E_{output} is the amount of energy expended or lost. In red deer, most of the energy intake (E_i) occurs as dietary energy (and some incident solar radiation). Energy output (E_o) can consist of energy lost by convection, conduction, radiation and/or evaporation (the environmental demand), that expended to maintain body basal metabolism (the BM requirement) or in muscular work (activity expenditure). The energy content of the body also may be increased by biomass production: by the production of new body tissue (growth and fattening), milk (lactation) or offspring (reproduction). The loss of energy by the hinds of this study shows that they were in a state of negative energy balance (E_{intake} was less than E_{output}), so that they were forced to katabolise body tissues to meet the deficit; with the final result being the losses in body weight which occurred as these tissues were destroyed. It can be hypothesised, therefore, that the weight loss could

have been avoided if the hinds had been provided with a supply of dietary energy equal to the amount (which has been established) they were losing from their bodies. Unfortunately this is not the case. No biological transfer of energy is ever 100% efficient (except for the relief of cold stress; see discussion in the next section), some energy always being lost as heat. In order to know the amount of energy that would be required by hinds to halt winter weight loss, it therefore is necessary to know the efficiency with which they expend body reserves, which requires knowledge of the processes upon which body energy is used, and also the efficiency with which dietary energy would be used for these processes.

7.2.1 EFFICIENCY OF ENERGY UTILISATION.

The efficiencies with which animals utilise energy is dependent on many factors. Efficiencies can vary between species, and within species between animals of differing genotypes, ages, previous nutritional histories (and hence levels of body condition), or metabolic healthiness: efficiencies can vary according to the energy source (e.g. diet or body reserves), and between types and concentrations of diet: efficiency of use of dietary energy can also depend on the type of energy to which referred. Moe and Tyrell (1973; quoting Harris, 1966) have outlined the terminologies in common use to describe types of dietary energy:

'dietary gross energy' is the gross energy content of a diet; when the faecal energy loss is subtracted from DGE,

'apparently digestible energy' is the result; which, when urine and methane losses are subtracted, becomes

'metabolisable energy' (ME). When the energy loss

through heat production is subtracted from ME, the result is the

'net energy for production' (NE_p). Moe and Tyrell also have pointed out that the efficiency of dietary energy use varies according to the physiological function for which it is expended, and suggested that ME is used for the following functions with efficiencies approximating those shown:

cold stress	100%
maintenance	70 to 80%;
lactation	60 to 70%;
growth	40 to 60%;
pregnancy	10 to 25%.

Unfortunately, little is yet known about the efficiency with which animals can use energy provided by the katabolism of body reserves. MacDonald et al (1973) suggested that the efficiency of free energy capture when body fat is katabolised is about 45%. Moe et al (1971) have estimated that dairy cattle can produce milk by the katabolism of body reserves with an efficiency of 82 to 84%. Rattray et al recently (1974) mentioned the existence of evidence that sheep use energy from maternal tissues to support foetal growth more efficiently than they use dietary energy, but gave no values for this.

7.2.2 EFFICIENCY OF ENERGY USE FOR PREGNANCY BY RUMINANTS.

Various estimates of the efficiency with which different species of ruminants use metabolisable energy (ME) for reproduction have been published in recent years. Russel et al (1967) estimated that Scottish blackface sheep utilised ME for production of the conceptus (foetus, foetal membranes and uterine fluids) with an efficiency of around only 5%, while Rattray et al (1973b) found that white-faced ewes in

the U.S. used ME for this process with an efficiency of 13%. Moe et al. (1970) estimated efficiency of ME for conceptus production in dairy cattle to be 11.5%, and Henseler et al (1973) have reported that the dairy cattle they investigated used ME for the conceptus with an efficiency of 14.9%.

Rattray et al (1974) have determined the efficiencies of use of ME by Targhee ewes not only for production of the conceptus, but also for that of the foetus alone, and the overall efficiency of use for pregnancy (deposition in the conceptus, uterus and mammary gland). Rattray et al's finding were 16%, 12.5% and 12.2%, for the processes of pregnancy, conceptus and foetal production, respectively. Rattray and his colleagues point out that the efficiency with which animals use ME for pregnancy is so low only when one considers the process as a storing of energy; no account is normally taken of the fact that energy is also being used for maintenance of the conceptus. (Rattray et al. estimated that ME was used for conceptus maintenance with an efficiency between 70 and 80%).

7.2.3 ESTIMATION OF THE ENERGETIC COST OF CONCEPTUS DEVELOPMENT.

Although the comments of Rattray and his colleagues on the efficiency with which their sheep used energy for maintenance of the conceptus are interesting, they do not change the fact that a pregnant animal must provide energy during foetal development at an ever-increasing rate, and that the efficiency of the overall process is only in the order of 16%. Since Rattray et al. (1974) intentionally attempted to ensure that maternal tissues were utilised for the production of the conceptus in their study, it seems legitimate

to assume that the efficiency of utilisation of energy by red deer for production of the conceptus is not too dissimilar (from 12.5%). If this be the case, the hinds of this study would have had to be expending energy on the growing conceptus at a rate of 22.5 kcal/day until around the 15th of March, and at around 0.574 Mcal/day after that date.

The accurate estimation of the efficiency with which hinds can use energy is important to the calculation of the overall energetic costs of pregnancy, as is demonstrated by the following considerations. The estimated efficiency of use of dietary metabolisable energy for conceptus development, by the dairy cattle of Henseler et al. (1973), was 14.9% (as compared to 12.5% found in sheep by Rattray et al, 1974). Use of the value from cattle estimates that, during the last third of gestation, red deer hinds need to provide 481 kcal/day to the developing conceptus; 92 kcal/day less than the estimated requirement employing the efficiency found in sheep. Thus the choice of which efficiency to employ can result in a difference in estimates of 16%. The value found for sheep is preferred in the estimate of red deer requirements, for the following reason: the apparent efficiency with which energy is used for development of the conceptus is based on comparison of the energy intake of an animal, with the amount found to be deposited in the conceptus. The greater the energy retention by the conceptus, the greater the efficiency assigned to the process. It has been clearly demonstrated in this thesis that the energy content of an animal (or biological product) is greatly affected by the amount of fat which is present in

the animal (or product). The composition of the foetuses of the cattle of Henseler et al. (1973) has been reported by Henseler and Jentsch (1973); at term, the foetuses had a fat content of 14.8% in DM, and an energy content of 5.09 kcal/g DM. The foetuses in the present study contained less fat (the average content in the last 4 collected was only 5.98% of the DM), and the energy in their DM content was correspondingly less (averaging 4.49 kcal/g DM). Admittedly, fat, energy and DM content are rising rapidly immediately prior to parturition, so that the comparability of the composition of the deer and cattle foetuses depends on how near to term the deer foetuses were. Nevertheless, it would appear that the foetuses of the dairy cattle of Henseler et al. contained considerably more fat (and therefore more energy) than do newly-born sheep or red deer. I suggest that because of this, the energetic efficiency of conceptus production was greater in these cattle than it is in red deer, and that the value established for sheep is more applicable to deer.

7.3 Estimation of pregnancy requirements, and the additional energy required to avoid winter weight loss.

7.3.1 PREGNANCY REQUIREMENTS FOR METABOLISABLE ENERGY.

If the estimates made in the previous section are close approximations of the true energy requirements of red deer for conceptus production, an indication of the total cost of pregnancy may be obtained by including estimates of the heat production by the conceptus. Using the value of 85 kcal of heat produced per kg conceptus per day (Rattray et al., 1974), heat production by the conceptuses of the hinds of this study is estimated to have risen from around 468 kcal/day in

late March to around 803 kcal/day at the end of May (see Table 7.3 for the weights of the conceptuses of the hinds collected after the middle of March). Thus the total energy the hinds would have had to be providing during the last third of gestation, will have increased from around 606 kcal/day in late March to around 1578 kcal/day at the end of May (these estimates have been arrived at by adding the estimated cost of energy deposition in the conceptus to the estimated energy lost as heat). In comparison, Rattray et al. (1974) estimated that, at Day 140 in gestation of the sheep foetus, a ewe bearing a single foetus would require around 1610 kcal of ME to meet the requirements of the conceptus and the developing mammary gland. The efficiency with which animals use body energy reserves for pregnancy may be greater than that for the utilisation of dietary ME; if so, the total energy cost to wild red deer can be expected to be somewhat lower than the requirement for ME in the diet.

7.3.2 PREGNANCY MINERAL REQUIREMENTS.

As stated in section 3.1.5 of Chapter 3, no indication was found that the relative amounts of the major mineral nutrients in the DM of the hinds decreased over the period of collection; indeed, the only indicated changes were slight rises in the percentages of the minerals in the DM. Although the estimated weights of sodium and potassium significantly decreased over the collection period (section 5.4, Chapter 5), the reason for this appears to be the loss of soft tissues, within which these elements are almost exclusively contained. If the mineral requirements of the growing conceptus were not being met satisfactorily, the

percentages of the minerals in deficient supply would have been expected to drop in the DM of the hinds, as they were mobilised from the mothers' bodies to be deposited in the foetuses. As there was no indication of this happening, it is assumed that dietary availability of the major minerals was sufficient to meet the rates of deposition as shown in Chapter 6, sections 6.3.1 - 5.

7.3.3 ESTIMATION OF WEIGHT MAINTENANCE REQUIREMENTS.

As has been pointed out in sections 7.2.2 - 3 and 7.3.1, it is not possible to estimate the energy requirements of wild red deer for pregnancy with confidence, since the energy content of the whole gravid uterus can be only estimated, and the energy cost of pregnancy cannot be known until the efficiency with which energy is utilised for it is established for deer. Furthermore, it is not possible to estimate, with confidence, the amount of energy which hinds would require to avoid body weight loss over the February-May period, since the physiological functions on which they are forced to expend body energy are not known. However, prior to mid-March, the demands of pregnancy appear to be low, so that the energy hinds are losing during February/mid-March must be being expended largely on basic metabolic maintenance, maintaining body temperature and in muscular activity. Silver et al. (1971) found that at ambient temperatures of -13°C., fasting white-tailed deer raised their heat production to nearly twice (to 138 kcal/kg body weight -$BW^{-0.75}$) the interspecific mean for homeotherms (70 kcal/kg $BW^{0.75}$). Since these deer were not being fed, the energy they expended in raising their heat production will have been supplied entirely from endogenous sources.

Wesley et al. (1973) found that the heat production (and so, energy expenditure) of pronghorn antelope (Antilocarpa americana) increased by 58% over fasting heat production, when the animals were allowed to endulge in 'moderate' activity. Unfortunately, the efficiency with which the animals made these expenditures from body reserves are not known. If it be assumed that red deer katabolise body sources for these processes with an efficiency similar to the generally accepted value for efficiency of use of ME for maintenace by domestic ruminants (72%; A.R.C., 1965), the actual deficit which the hinds of this study were experiencing will have been around 404 kcal/day (i.e., 72% of the 561 kcal the collected hinds have been found to be losing per day). However, it seems probable that endogenous energy sources are utilised with a greater efficiency than this, possibly ranging from around 82 to 100% (for maintenance of body temperature the efficiency will be 100%). If this be the case, the hinds will have required a supply of from 8.3 kcal (which is equivalent to 34.8 kilo-Joules, kJ) to 10.1 kcal (41.9 kJ) of dietary ME per kg of live weight (including the conceptus weight) per day, in addition to whatever amount of dietary energy they were receiving, if they were not to lose weight over the February-May period.

7.4 The maintenance energy requirements of ruminants.

Estimates of the energy requirements of different species of ruminants have been found to vary considerably. Rattray et al. (1973a, b) have estimated the maintenance requirements of sheep to be from 103 kcal of ME/kg $BW^{0.75}$/day (1973a) to 120 kcal ME/kg $BW^{0.75}$/day (1973b). Moe et al. (1970) es-

timated that the ME requirement for maintenance of lactating dairy cows was 122 kcal/kg $BW^{0.75}$/day, compared to only 100 kcal/kg $BW^{0.75}$ for non-lactating cows. This agrees with the estimates of Neville (1974), that the ME maintenance requirement of lactating Herefords (174 kcal/kg $BW^{0.75}$/day) was greater than that of dry animals (123 kcal per kg $BW^{0.75}$). Stanley Price has recently (1978) estimated the fasting metabolic rate (FMR) of Coke's hartebeeest (Alcelaphus buselaphus cokei) to be 215.6 kJ/kg $BW^{0.73}$/day (which is equivalent to 52 kcal/kg $BW^{0.73}$); if the hartebeest uses ME for maintenance with the efficiency of 72%. its requirement will be around 72.2 kcal ME/kg $BW^{0.73}$/day. Stanley Price points out that, unlike most wild ruminants, the wildebeest's FMR appears to be below the inter-specific mean, and suggests that this is an adaptation by the animal to its arid environment. Rees (1978) has estimated that another African ruminant, the lechwe (Kobus leche kafuensis), if of an average weight of 66 kg, wouldhhave a maintenance requirement of 3.1 kJ ME per day.

Nordan et al. (1970) estimated that the fasting heat production (FHP) of young female black-tailed deer (Odocoileus hemionus columbianus) was 149 kcal per kg $BW^{0.75}$. McEwan (1970) estimated the heat production of caribou females (Rangifer tarandus) at 'the maintenance level of feeding' to be 115.8 kcal/kg $BW^{0.75}$/day. Silver et al (1969) found the FHP of white-tailed deer, kept outside and exposed to normal temperatures, to have an average value of 97.1 kcal/kg $BW^{0.75}$ per day during winter (= 33.8 kcal/kg body weight), and assuming white-tailed deer use ME for maintenance with the efficiency of 72%. the winter maintenance requirement

of these beasts would have been around 135 kcal ME/kg $BW^{0.75}$. Ullrey et al. (1970) estimated (by regressing estimated ME intake on body weight change) that pregnant female white-tailed deer required 131 kcal of ME/kg $BW^{0.75}$ per day to avoid losing weight over the period February to April. Holter et al. (1977) studied the nutrition of white-tailed deer throughout the first year and a half of life. Their animals, like those of Silver et al. (1969) and Ullrey et al. (1970), were kept in open pens outside, and Holter and his colleagues estimated the requirements of their deer for weight maintenance to be 153 kcal ME/kg $BW^{0.75}$ per day. The larger size of this estimate, as compared to that of Ullrey et al., is presumably a reflection of the younger ages of the deer of Holter et al. Age presumably also is the explanation for the difference in the estimate of Simpson (1976), of 539 J of ME/kg $BW^{0.75}$/day (= 130 kcal ME/kg $BW^{0.75}$) for young red deer stags measured indoors, as compared to the estimated requirement of 125 kcal ME/kg $BW^{0.75}$ by the red deer hinds examined by Brockway and Maloiy (1968: calculated by me on the assumption that the average heat production at 18°C., 90 kcal/kg $BW^{0.75}$, could be supplied by dietary ME with an efficiency of 72%).

7.5 Summary and discussion of deer energy requirements.

7.5.1 PREGNANCY REQUIREMENTS.

Estimates of the amounts of energy required by wild hinds for pregnancy are dependent upon assumptions being made about the efficiency with which the animals use energy for the various parts of the process, estimates made of the energy contained in the whole gravid uterus, and of heat production by it. The foetuses collected in this study were found to

be increasing in energy content at a rate of around 2.66 kcal/day (95% confidence limits for this regression coefficient are 0.118 to 5.20 kcal/day) prior to the middle of March. After mid-March (the beginning of the final third of the gestation period), energy was retained in the foetuses at a rate of around 64.09 kcal/day (95% limits: 48.60 to 79.58) (Table 7.2). The estimated rates of deposition of energy in the whole conceptus are 2.81 kcal/day (-0.586 to 6.207) until mid-March, and 71.72 kcal/day (53.77 to 89.68) from then until parturition.

If red deer deposit energy in the conceptus with an efficiency similar to that of sheep (12.5%), the estimated rates of energy expenditure for conceptus development are 22.5 kcal/day (4.7 to 49.7) up to mid-March, and 573.8 kcal/day (430.1 to 717.4) afterwards, till term. Total energy requirements for pregnancy have been roughly estimated to rise from around 606 kcal/day at the beginning of the last third of the gestation period (late March) to around 1578 kcal/day near the end of May. It must be emphasised that these are only rough estimates of the energy requirements of red deer for pregnancy, based on a number of assumptions about efficiencies of energy use, the validities of which are unknown.

7.5.2 ENERGY REQUIRED TO AVOID WINTER WEIGHT LOSS.

The estimation of the amounts of energy the hinds of this study would have required to avoid losing weight, requires assumptions to be made about for what the energy (that it has been shown they were losing) was being expended. The hinds were found to be losing energy from their bodies (not including the contents of the uterus) over the period 14 February

to 25 May at an average rate of around 560 kcal (or 7.3 kcal/kg of live weight, including weight of the conceptus) per day. Curiously, the rate of loss appeared to be linear over the whole of the period, in spite of the increasing demands made for energy by the growing conceptus as term approached. It may be that the environmental demand had sufficiently decreased (and dietary energy intake perhaps increased) at a rate equal and opposite to the increasing demand of pregnancy.

If the energy lost by the hinds in the first half of the collection period is assumed to have been expended on body maintenance, homeothermy and muscular work, the efficiency of tissue katabolism for this is assumed to have been from 82 to 100%, and dietary energy to be used with an efficiency of 72% to meet these functions, estimated requirements to avoid winter weight loss are for a supply of dietary ME of from 8.3 kcal (34.8 kJ) to 10.1 kcal (41.9 kJ) kg of live weight per day, in supplement to the energy intake that the animals were already receiving. These requirements presumably would increase considerably during the final third of pregnancy, although there was some evidence that hinds may be able to acquire sufficient dietary energy, by late May, to begin to recover condition, and, therefore, body weight (see Chapter 5).

7.5.3 TOTAL ENERGY REQUIREMENTS OF RED DEER HINDS IN WINTER.

Because neither the energy intake which they were receiving, nor the efficiency with which the body energy they lost was used are known, it is not possible to state what the energy intake of the hinds of this study was, nor what

their total requirements during winter are. However, the data of Ullrey et al. (1970), Brockway and Maloiy (1968) and Simpson (1976), in combination, seem to suggest that both white-tailed deer and red deer require a daily dietary intake of around 131 kcal of ME per kg $BW^{0.75}$/day (543.4 kJ of ME) if body weight is to be maintained. Since the value of Ullrey and his colleagues was estimated from deer living outdoors, subjected to normal winter weather and undergoing body weight losses, it seems likely to be a reasonably accurate estimate of maintenance requirements. The requirements of wild red deer, on the open hill during winter, may be considerably greater than the values estimated by Brockway and Maloiy, and Simpson, due to the need to increase body heat production during periods of cold weather (Silver et al., 1971), and the costs of normal activity (Wesley et al., 1973). If the total requirements of wild red deer hinds are similar to those of the deer of Ullrey et al. (1970), the hinds of this study must have been acquiring a dietary intake of around 100 kcal of ME/kg $BW^{0.75}$/day (130 $kcal_{maintenance}$ - 30 $kcal_{lost}$). This would mean that a hind weighing 70 kg would have a total requirement of around 3.29 Mcal (13.65 MJ) of ME per day. The hinds of this study would have been receiving around 2.40 Mcal (9.949 MJ) per day.

The results reported in this dissertation were used as the basis of an attempt to assess experimentally the effects of energy intake and expenditure on the productive performance of wild red deer hinds. The experiment involved providing wild hinds with a prepared diet (of a ME content

established for cattle) during the winter/spring period mid-February to June; estimating their dietary ME intake from this and their natural food resources; estimating their expenditure to meet environmental demand; and measuring their productive response. A brief description of this attempt is given in the next chapter, along with a discussion of some of the reasons for its lack of success. Also presented are some thoughts on the implications of the findings reported in the previous chapters for the attempt to improve the biomass productivity of red deer in the Highlands. Finally, some areas of further research are suggested.

CHAPTER 8. Improving the Biological Productivity of Wild Highland Red Deer.

The results reported in the previous chapters (the analyses of the hinds and foetuses that had been collected in this study) were used as the basis of a field experiment into the effect of providing high-energy content supplementary feeding to wild hinds during the period mid-February to June. A report on this work already has been submitted to the Highlands and Islands Development Board, (which provided most of the money for this research). Because the experiment was inconclusive, it is described in this chapter in outline only. The chapter also includes a brief discussion on some of the implications of the results of this study (as reported in the previous chapters) for possible practices aimed at improving the biomass productivity of wild Highland red deer. Finally, some areas of further research are suggested.

8.1 The feeding experiment.

8.1.1 OBJECTIVES.

The objectives of the experiment undertaken were to try to establish the productive response of wild red deer hinds to the input of an estimated amount of dietary metabolisable energy (M.E.); and to investigate the practical problems of feeding wild hinds during the winter.

8.1.2 EXPERIMENTAL DESIGN.

The feeding experiment was carried out in Glenstrathfarrar, a glen running west to east with the top of its northern ridge marking the border between the then counties of Ross-shire (to the north) and Inverness-shire. This

glen was chosen because of the number of large coires (corries, or miniature valleys) located in the northern ridge of the glen (the coires running north-south, perpendicular to the main glen). Originally it was intended to feed a group of about 30 hinds which were hefted to the ridge forming the western side of Coire Mhuilidh about two-thirds of the way to the top of Glenstrathfarrar (the main territory of these hinds was on either side of the ridge, rather than the coire itself), and to compare the performance of this group of animals with that of a control group, hefted to the ridge forming the western side of a coire about 5 km further west, at the head of the glen. (This choice was made in consideration of the need to have at least relatively easy access to the coires, and the assumed need to have some separation between groups: the two areas were separated by two ridges and an intervening coire which was inhabited largely by stags). The productive response of the group to be fed was to be assessed by comparison with the control group in respect of:

(i) calf/hind ratios;

(ii) birth weights of calves;

(iii) larder weights of hinds, and assessment of their condition during the normal stalking season following the winter(s) of feeding;

(iv) to weigh an equal number of control and to-be-fed beasts at the beginning of the experiment, so that their growth rates (weight changes) could be compared.

It was intended that the dietary energy intake of the two groups be estimated by estimating the M.E. content of the natural vegetation, and consumption rates of it. Details of

incoming radiation, air temperature, rainfall and wind speed were recorded at sites at the top and bottom of the east faces of the ridges on which the deer were hefted. It was intended to complete a computerised mathematical model describing energy loss due to environmental demand (Anderson, 1972), and to use the gathered weather data in this model, to predict the demand experienced by the two groups of deer (or at least to achieve an objective index of weather severity, depending on the reliability of the model to describe the real environmental demand).

8.1.3 THE FIELD EXPERIMENT.

I originally planned to put out feed on a grassy slope on the east-facing face of the ridge occupied by the animals to be fed (where the hinds had been observed to spend considerable time, during the winter previous to the beginning of the experiment). Due to the exceedingly mild, open weather during the first winter of putting out food (1974), the hinds that year spent little time in the area of the feed, and (presumably because they therefore did not come into contact with it for long enough), the feed was not eaten by deer at that area. Hinds did feed on food that was put out in the main glen (at the point where the ridge forming the western side of Coire Mhuilidh joined the main glen), but this area did not fit the experimental design, in that hinds came from several parts of the glen to congregate there at night. It therefore would not have been possible to segregate, feed and study only that hind group which had been selected (more hinds could not be fed, because of financial limitations).

Although the work of the first winter of the experiment was not a success, it had shown that it was possible to get wild hinds to accept this particular artificial feed, but that this must be done in a place where the hinds regularly congregated. In the winter 1974/75, therefore, another group of hinds was chosen to feed. This group also came down into the main glen at night, but in an area where they were not joined by other hind groups. The new group was hefted on the ridge making the east side of Coire Mhuilidh, so that the hinds which it was originally intended to feed (hefted to the western ridge of the coire) were re-designated as the control group. (This was done because there seemed to be little or no mixing of the two groups, and the lack of time to try to perfect the environmental energy demand model made it desirable that fed and control groups experienced similar weather conditions).

The numbers of the new group to be fed varied occasionally, but seemed to consist basically of 16 hinds and 4 calves. Some of the members of the group had been observed previously to feed on kitchen scraps thrown from a house in the glen. The group had been selected partly for that reason; because they appeared to be accustomed occasionally to eating novel items, I thought they might start to accept the experimental feed sooner than other deer. This assumption was proved correct when the hind, later identified to be the leader of the group began to eat the feed on the first occasion that it was put out. At least half of the entire group appeared to be feeding within a fortnight. Feed was put out almost daily from 13 February until mid-May, at which time the hinds ceased to come each night to the feeding area

(presumably because of the end of winter, and perhaps because of the approach of the calving season).

Over the total feeding period approximately 1100 kg of the supplementary diet was consumed (the daily average was 11 kg for 100 days).

Great difficulty was experienced by the veterinary surgeon who contracted to immobilise the fed and control hinds to be weighed and marked. The method employed involved the use of syringe projectiles, containing an immobilising drug, fired from a gun. Largely due to the limited range (around 50m) and general unreliability in the accuracy of the projector, only 4 fed and 4 control beasts were ultimately darted, in spite of the expenditure of over 60 man-hours by the veterinary surgeon. The animals which were immobilised were weighed and fitted with identifying Dalton cattle collars.

In addition to attempting to assess the hinds, recently-born calves were caught from what were assumed to be the fed and control groups, over three calving seasons. The calves were weighed and heart-girth measurements taken, after which they were tagged in both ears with Dalton brand 'Jumbo' tags.

I recorded the larder weights of unfed hinds, culled during the stalking season (1975/76) following the winter of successful feeding but because it proved possible to cull only one marked (and therefore known) feeder hind, the experiment was virtually without result. The failure to shoot the other three marked feeder hinds was not the result of a lack of trying, but the ground they occupied during the stalking season was particularly unsuitable for successful

stalking. Thus, in spite of repeated attempts, only the one hind was recovered. (An element of human resistance to shooting the known feeders was also encountered, since the animals, being marked with collars, were readily and individually identifiable, and came to be regarded rather as the pets of the glen).

Although a sample of one can be accredited with no scientific value, it is of interest to report the measurements made on the one known feeder hind which was recovered during the taking of the cull. The age of the animal when she was immobilised and collared (as subsequently estimated from the state of tooth wear) was 4 years. At that time (21 March, 1975) she had a live weight of 68.5 kg. When shot the following season (on 16 January, 1976, when she was an estimated 5½ years old), the hind had a live weight, less the loss of some blood, of 80.0 kg, and a larder weight of 61.2 kg. The hind therefore had undergone an apparent increase in live weight, over a period of 10 months, of 11.5 kg.

8.1.4 CONCLUSIONS ON THE FEEDING EXPERIMENT.

With the benefit of hindsight it does not appear surprising that the feeding experiment could not be brought to a significant conclusion. As the work progressed it became increasingly apparent that the size and scope of the project made it more suitable for a research team rather than a single individual (although considerable help was occasionally obtained from various people; e.g. during calf-catching operations).

Particularly difficult problems met with during the experiment included:

(i) finding a suitably discrete area in which resided a deer group small enough to meet the financial limitations on the amount of feed which could be offered;

(ii) being able to locate and catch the calves of the specific hinds which comprised the fed or control groups (this was much more difficult than catching calves at random);

(iii) being able to immobilise hinds in sufficient number (as already pointed out, over 60 man-hours were spent by a veterinary surgeon, for a success rate of only 8 beasts marked: the cost of this could have been enormous, and the need for the darting to be done by a veterinary surgeon, or at least with one in attendance, reduced the time that could have been spent on attempting to mark and weigh animals;

(iv) finding an objective method of measuring the condition (i.e. fatness) of live animals, even when immobilised; and

(v) overcoming the obstruction (both intentional, and unintentional by misconceived well-wishers) by various persons, to various aspects of the research.

The final solution to the problem of getting hinds to accept supplied feed simply was to place it in an area where the hinds regularly gathered (e.g., at particular places in the glen at night). The problem remained of the non-durability of the feed (which was in the form of a mixture of various ingredients made into a 'nut' - an approximately 0.5 cm-long segment of a cylindrical 'rope' - which would disintegrate after exposure to rain for more than even

a few hours). Thus fresh allotments of the feed had to be put out, virtually every day, until the hinds began to accept it, and a more durable form (e.g., whole maize) may be preferable for trying to start hinds on an artificially-provided feed. Had the experiment resulted in more hinds being marked and recovered, the problems would have remained of trying to estimate the M.E. which they had received from the vegetation in addition to that provided in the nuts, estimating the amounts of the feed which they had actually consumed individually, estimating the amounts of energy spent in activity, and that to meet the environmental demand.

The problem also existed of deciding at what point the effects of the feeding should be assessed. Since it was hoped that the experiment might be of immediate practical value, I decided to make the assessment in terms of increased weight and improved condition during the following shooting season (when impressive results might have been observed directly by deer managers). However, scientifically it was desirable to assess the effects on body weight, condition and energy content of fed hinds and their calves, both at the end of feeding (i.e., June), and at the end of the summer period of positive energy balance (when body reserves are being deposited): it would be of considerable value to establish the extent to which feeding improved weight and condition at the end of winter, in comparison to unfed beasts, and also to see how animals with this initial advantage put on weight and condition over the summer, relative to un-fed animals.

Although of greater feasibility at the conception of the project (the price of foodstuffs trebled within the

first 18 months of the experiment), the practical prospect of trying to improve the biomass production of Highland red deer by winter feeding is not particularly attractive ecologically (see further discussion in the following sections). However, it is unfortunate that the experiment was inconclusive, since its possible results remain of considerable practical and scientific interest. Very few studies have attempted to measure the energy dynamics, and the effects of these on production, of wild or domestic ruminants in a natural grazing environment. Although the problems of estimating with confidence the energy intake and expenditure of the fed hinds remained unresolved, the failure of the experiment to come to any conclusion of scientific value is regrettable. The work did, however, clearly demonstrate the many difficulties inherent in trying to mark, assess and recover large wild animals.

8.2 Possibilities of improving the productivity of Highland red deer.

The rates of loss of fat and energy from the bodies of the hinds collected during the first part of this research, and the very low levels of body fat remaining in the beasts taken at the end of May (less than one kg of chemical fat), well may make one wonder how Highland hinds manage to survive and successfully produce offspring (not to mention the fact that some do so while experiencing the energetic cost of lactation as well) as often as they do. Yet, not only do red deer regularly survive and reproduce, but if official Government opinion is accepted, the population of the whole of the region has increased at a remarkable rate in recent years. Be that as it may, it remains the case that red

deer in the Highlands presently are subjected to little 'management' other than the annual shooting with a rifle of a percentage of the estimated populations. Little effort (if any) is being made consciously to increase the biomass production of the species, either by manipulation of the animals, their populations or habitats (excepting perhaps casual burning of the hill vegetation; this, however, is more often an act of faith - 'it's good for the deer' - than a scientifically tested and applied management technique). It may be proposed that this is desirable: that man is over-keen to manipulate one of the few remaining 'natural' areas, and animals, in the British Isles. This naturalistic argument seems to be invalid, however, not only because hardly any land in the Highlands has escaped considerable modification by man or his domestic stock, but also because evidence from all parts of the world suggests that unless it can be shown that, for example, red deer and the ground they occupy are actively (although not necessarily scientifically) managed, both are liable to increasing competition from other forms of land use. This is especially the case in Great Britain, which is so grossly over-populated (to the extent that insufficient land and other natural resources are available to maintain the population at the continually increasing standard of living its people expects). This is not necessarily an argument against alternative or co-existing forms of land use being introduced into the Highlands at the expense of wild deer. However, on much of the high ground, intensive systems of forestry or animal husbandry (of traditional domestic, or red deer, stock) do not appear to have much chance of being commercially viable.

In any case, amongst various options possible for Highland land use, it yet has to be shown that extensively managed red deer populations cannot markedly increase their biological productivity.

One of the particularly inhibiting features of Highland deer productivity is the large proportion each year of 'yeld' (i.e., barren) hinds. The biologically more efficient method of converting plant energy into humanly-consumable animal products (fat or protein), appears generally to be by the production of many (even if of smaller size) animals, rather than a few large ones. Thus it may be suggested that the biomass production of Highland red deer best might be increased by increasing the number of deer produced annually (and one way to do so is to reduce the number of adult, non-breeding hinds). Such a procedure need not lead to an increase in the present population size; it could be applied to any population level without increasing its overall size, by increasing the culling rate to the level of the increased reproduction rate. It also need not interfere with the management objective of concurrently producing shootable 'trophy' stags, since stags and hinds often do not occupy the same areas of ground, and appear to use different portions and vegetation types when they are on the same area (see Jackes, 1973; Mitchell et al., 1977). Furthermore, a reduction in the number of stags may actually lead to large size in the remaining animals, if this reduces competition, either socially or for the limited energy available (fewer stags also might increase their commercial value, simply because of their rarity).

The problem yet has to be solved of how it may be possible to decrease the number of yeld hinds and so increase the reproduction rate. Mitchell (1973) has proposed that the present birth rate in the Highlands is almost 40 calves/100 hinds, and pointed out that this is due largely to the high proportion of hinds which take a full year to recover from the stress of pregnancy and lactation. Mitchell et al (1977) refer to an estimate that in one red deer population in the Highlands, 30-40% of the sexually-mature hinds failed to ovulate or to conceive in a given year. The considerable losses in chemical fat (from around 28 to less than 8% in the body DM content) and in body gross energy content (from around 130 Mcal to around 70 Mcal, a loss of over 50%) sustained by yeld hinds between mid-February and the end of May, demonstrate that hinds are subjected to a large deficit over the winter and spring period. However, these findings, in conjunction with the evidence of extreme winter weight losses in white-tailed deer in some areas of America (e.g., Silver et al., 1969; Ullrey et al., 1969, 1970) also may be interpreted as evidence that deer of these species are particularly well-adapted to maintaining themselves, and producing offspring, by the katabolism of body energy reserves over the winter. Indeed, it is a failure to gain sufficient body weight and condition over the summer months which causes a hind to fail to conceive, or to conceive so late that the resulting late birth date of the calf prejudices its prospect of surviving its first winter. Furthermore, the data of Mitchell et al. (1976) has shown hinds which are yeld to be most similar, but superior to milk hinds in body weight and condition at the end of April. The situation is the same two months later (i.e., yeld are

superior to milk in early July). However, the condition of individual hinds, relative to each other, may well have been reversed in this short time: i.e., a hind that was yeld and superior in condition in April, will probably be a milk hind (since she has a better than 90% chance of having been pregnant and so now lactating; Mitchell et al. 1977) by July, and be poorer in condition than the 30-40% of hinds which were previously 'milk', but were not pregnant, and therefore have now become yeld hinds.

My impression, gaining strength through the present research, and from publications on red deer in recent years (e.g. Blaxter et al., 1974; Mitchell et al., 1976; Mitchell et al., 1977), is that Highland red deer are physiologically well-adapted to utilising body energy reserves to survive and reproduce over the winter. This view, and the fact that a hind which has begun lactating in early summer has a 30-40% chance of achieving insufficient weight and condition to ovulate the following autumn, lead me to the opinion that the dietary energy available during the summer months is the most important single factor inhibiting the reproduction, and therefore, biomass productivity, of Highland red deer.

8.3 Càit a bhitheas againn ri dhol a nis?.[1]

To come to the firm conclusion that any particular part or process of a biological system is of 'PRIME' importance is a state of mind of which any ecologist ought to beware. However, the assertion that summer level of dietary energy is the single factor most inhibiting the productivity of wild Highland red deer, does not diminish

1 "Where do we go now?"; Highland Gaidhlig (Gaelic)

the importance of other factors. Indeed, the essence of the ecological (as opposed to any other type of biological) approach is to attempt to identify the factors of most importance, in their effect on the biological process of interest to the investigator, while not disregarding the interaction of other factors.

8.3.1 AREAS FOR FURTHER RESEARCH.

If it be the case that Scottish red deer have become naturally adapted to an annual cycle of gaining body energy reserves (largely fat) during the summer and living off these reserves during winter, the wisdom of employing certain techniques, that in the light of the findings of this research may seem obvious, require careful consideration. For example, an attempt to boost deer productivity by the provision of winter feeding (as may seem logical, in view of the extreme losses of body energy the hinds in this study were found to be experiencing), may be not only ecologically objectionable (since it entails a large energetic - and capital - input from outwith the system), but also unnecessary. At least this may not be the most efficient method that could be employed to achieve the goal of increased production. However, the finding by Anderson (1972) that winter weather parameters could account for over 90% of annual variation in the percentage of the population of Rhum red deer dying 'naturally' indicates that the occasional provision of winter feed, to prevent the very wasteful periodic heavy mortality that can occur in late winter and spring, could be of value. Further research is needed to develop methods of predicting the effect of weather, in any given winter, on the level of

mortality likely to occur the following spring. Thus deer managers might be forewarned that the provision of some level of feeding would be desirable. (Evidence has been found recently against the opinion that deer, having reached a certain critical stage of under-nutrition, will die even if good quality feed be provided. Twelve out of 13 female mule deer which had been starved completely, experimentally, for 10 to 64 days, failed to die as expected, after re-feeding: deCalesta et al., 1975, and deCalesta et al., 1974, have shown that deer maintain viable and functioning rumen bacteria, in abundance, after 4 to 47 days of complete denial of dietary intake. Recently - 1977 - the same authors found that of 8 deer fed only 25% of the amount consumed by a control group for 6 weeks, and then denied all food for a period of 23 days, 3 of the animals died. All the 5 surviving deer, when fed ad libitum at the end of 6 weeks of gross undernutrition and 23 days complete starvation, consumed three times as much as the controls, and soon regained normal health. These results show that the deer are much more resilient than is sometimes thought). However, research is also desirable as to the type, level, and period of feeding in order to avoid a predicted heavy spring mortality among deer.

Since energy balance appears to be more inhibiting Highland red deer production at the moment than other nutritional factors (the situation may change, if energy supply is increased, so that deficiency of other nutrients becomes more inhibiting), research into all aspects of the energy dynamics of the animals would be of some value. Easterbee and Grace (in press) recently have made estimates, from a

theoretical physical model and actual measurements of wind profile over a Highland glen, of the loss of energy due to forced convection and radiation by deer standing or lying on the open hill, as compared to that when the animals are in a wooded area. Such research is of value, since it is desirable to have quantitative evidence of the advantages of reducing energy loss by the provision of shelter. An advanced form of energy balance has been begun recently with white-tailed deer. Holter et al. (1976) have reported on the beginnings of an attempt to implant a device into wild deer, which would be capable of taking measurements of various physiological parameters and broadcasting these data by telemetry. Some work of this kind involving considerable technological expertise has been advanced by the Wolfson Microelectronics Unit at the University of Edinburgh. Although such a study could be of immense value and ought to be undertaken, its complexity emphasises a pitfall which perhaps has not been avoided often enough in the past; that of research resulting in little value to managers of red deer. I do not mean to imply that the use of advanced technology [illegible] ought not to be used in red deer research, and think that such a physio-telemetry study on wild deer has tremendous potential. However, if one's objective be to provide the basis for advice on management techniques, there is a danger of becoming overly-involved, for too long a term, in a line of research which ultimately is only of limited practical value.

As well as investigating the energy output which Highland deer must undergo, studies of dietary intake could be

of value. Research into the energy intakes, availability, metabolisable energy content, and how these change with season, are required on the major species of deer food plants. The possibility of improving parts of the summer range, for instance by fertilising and re-seeding selected areas, is also a possible method of increasing the productivity of deer. However, types of fertilisation and plant species best to employ, optimal areas to treat, how to place such areas so that the plants will survive, at the same time not causing harmful disruption to normal deer distribution, and several other aspects require investigation. Furthermore, before investigations are begun which involve considerable manipulation of the deer or their habitat, it would be wise to have first investigated the present situation more fully. The answer to improving red deer production in the Highlands appears to be to improve their energy balance, and in particular their summer dietary energy intake. Energy balance can be improved by decreasing output, or increasing input. Physiological studies to quantify why some hinds do not improve in condition sufficiently over the summer should be given a high research priority.

Finally, any attempt to increase deer productivity, by increased intensity of management, will require more precise information of the home ranges and movements of Highland red deer. As Mutch et al. (1976) have pointed out, present estate boundaries often bear no resemblance to the pattern of use of the ground by the deer. In order for the management of Highland red deer to be improved to any great extent, it is essential that proprietors, and their managers, define the limits of the range used by their deer, and where this

overlaps boundaries drawn on a map, managerial co-operation will have to be achieved.

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